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Synecology and Autecology of Boreal Forest Vegetation in the Alberta Oil Sands Environmental Research Program Study Area

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ALBERTA OIL SANDS ENVIRONMENTAL RESEARCH PROGRAM
RESEARCH REPORTS

These research reports describe the results of investigations funded under the Alberta Oil Sands Environmental Research Program, which was established by agreement between the Governments of Alberta and Canada in February 1975 (amended September 1977). This 10-year program is designed to direct and co-ordinate research projects concerned with the environmental effects of development of the Athabasca Oil Sands in Alberta.

A list of research reports published to date is included at the end of this report.

Enquiries pertaining to the Canada-Alberta Agreement or other reports in the series should be directed to:

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Synecology and Autecology of the Boreal Forest Vegetation in the Alberta Oil Sands Environmental Research Program Study Area

Project LS 10.1

AOSERP Report 99

This report may be cited as:

Eulert, G.K., and H. Hernandez. 1980. Synecology and autecology of boreal forest vegetation in the Alberta Oil Sands Environmental Research Program study area. Prep. for the Alberta Oil Sands Environmental Research Program by Interdisciplinary Systems Ltd. AOSERP Report 99. 184 pp.

The Hon. J.W. (Jack) Cookson
Minister of the Environment
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Edmonton, Alberta

and

The Hon. John Roberts
Minister of the Environment
Environment Canada
Ottawa, Ontario

Sirs:

Enclosed is the report "Synecology and Autecology of the Boreal Forest Vegetation in the Alberta Oil Sands Environmental Research Program Study Area."

This report was prepared for the Alberta Oil Sands Environmental Research Program, through its Land System under the Canada-Alberta Agreement of February 1975 (amended September 1977).

Respectfully,

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Chairman, Steering Committee, AOSERP
Deputy Minister, Alberta Environment

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SYNECOLOGY AND AUTECOLOGY OF THE BOREAL FOREST VEGETATION IN THE ALBERTA OIL SANDS ENVIRONMENTAL RESEARCH PROGRAM STUDY AREA

DESCRIPTIVE SUMMARY

The development of the Athabasca Oil Sands area will result in the physical disturbance and destruction of sizeable areas of vegetation. Reclamation of these areas is a requirement of the lease agreements. In addition, vegetation in adjacent undisturbed habitats is subject to the impact of effluents with potential adverse effects. In order to successfully reclaim disturbed areas and monitor any subtle changes in natural vegetation communities, a knowledge of the synecology and autecology of the vegetation is required. Community successional patterns on undisturbed sites are of particular interest so that successional change induced by stress factors associated with development can be detected and their importance to ecosystem stability and productivity evaluated.

The purpose of this study is to describe the current state of knowledge concerning the synecology and autecology of the boreal forest vegetation in the AOSERP study area. This will include a problem analysis defining the necessary studies to obtain an understanding of the successional relationships of species and communities in order to predict the course of succession on reclaimed lands and apply this knowledge to species selection for reclamation purposes; and to identify any changes in succession due to oil sands development.

This report has been reviewed and accepted by the Alberta Oil Sands Environmental Research Program.

W.R. MacDonald, Ph.D
Director (1980-81)
Alberta Oil Sands Environmental
Research Program

SYNECOLOGY AND AUTECOLOGY OF BOREAL FOREST VEGETATION IN THE ALBERTA OIL SANDS ENVIRONMENTAL RESEARCH PROGRAM STUDY AREA

by

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for

ALBERTA OIL SANDS

ENVIRONMENTAL RESEARCH PROGRAM

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ABSTRACT

A review of the literature pertaining to the forest ecology of the Alberta Oil Sands Environmental Research Program (AOSERP) study area was completed.

Because of the complex nature of the vegetation pattern, the dynamic interactions of overstory species, and the relation of understory species to the nature and type of the canopy, the stands are discussed on the basis of relatively pure overstory species dominance. Dominant species examined were: aspen, jack pine, balsam poplar, paper birch, white spruce, black spruce, tamarack and balsam fir. The ecological factors discussed for each of these and 12 other understory species include soil and moisture requirements, reproduction, establishment, growth, successional roles, sensitivity to pollutants, and the nature of associated species.

Fire is the major disturbance factor of the boreal forest. Aspects of fire discussed are: the nature, causes, incidence and extent of fire; its influence on soil heat balance, soil pH, and nutrient availability; and the general effect on the vegetation mosaic. General dynamics of vegetation are discussed and summarized for muskegs and related wetlands, river and lake shores, uplands, lowlands and the understory.

The literature relating to North American concepts of communities, climax and succession is summarized to clarify usage of these terms and to illustrate the diversity of views that exist.

Five approaches to studying and classifying vegetation are discussed: (1) physiognomic classification; (2) the ordination (continuum) view of vegetation; (3) floristic classification; (4) the North American approach based on physiognomy and dominance, and (5) biophysical land classification. For each approach, a general description of its characteristics, data requirements, advantages, disadvantages and applications are discussed.

The report concludes with a discussion of data gaps and recommends studies needed to fulfill AOSERP objectives.

ACKNOWLEDGEMENTS

Appreciation is expressed to Dr. John Jeglum for his assistance in obtaining references and for his helpful advice.

This research project LS 10.1 was funded by the Alberta Oil Sands Environmental Research Program, a joint Alberta-Canada research program established to fund, direct and co-ordinate research into the effects of oil sands development on the renewable resources of the Athabasca Oil Sands.

1. INTRODUCTION

The Alberta Oil Sands Environmental Research Program (AOSERP) was designed to investigate effects of development of the Athabasca Oil Sands upon the physical and biological environment of the region. Knowledge of existing vegetation structure and function is necessary to provide baseline information for future reference, and knowledge of species and site dynamics is fundamental to understanding vegetation changes or succession through time. Local successional sequences can be a standard against which reclamation efforts may be evaluated, and could provide knowledge of alternative mechanisms to meet long-range reclamation objectives.

Current knowledge of vegetation dynamics on the AOSERP study area is limited and generally inferred from studies elsewhere in the region. Previous investigations on the study area have been concerned with the location and characterization of major vegetation types.

The study objectives were:

1. Complete a research review on the physiology and autecology of boreal forest species and on the structure of the vegetation communities in the boreal forest with particular reference to the AOSERP study area;
2. Complete an appraisal of the current literature applicable to the AOSERP study area for suitability for successional description;
3. Determine the detail of successional description and quantification required to meet AOSERP objectives and to identify any knowledge gaps in the literature; and
4. Recommend studies (as required) to meet the defined needs of AOSERP with special reference to bioproductivity, habitat type and quality, and vegetation indicator species or growth responses induced by oil sands development activities.

In addition, the contractual "outline of work" required: "Give particular attention to the successional relationships of species and communities that have been disturbed by development or natural catastrophic events",..."include emphasis on the identification and characterization of major communities, community-site relationships, and the ecological characteristics of important species", and "describe and evaluate systematic descriptions and organizations of boreal forest communities making comparisons of different systems for suitability to successional analysis in the AOSERP study area."

Initially, the important species were to consist of the eight major dominant trees but during the study it was expanded at the request of AOSERP personnel to include an additional 12 species.

The report was to cover the topics to the extent allowed by the available literature and within a level of effort of 3 man-months by professionals and 2 man-months of technician time.

Nomenclature of vascular plants follows Moss (1959); of lichens, Hale and Culbertson (1970); and of mosses, Crum et al. (1973).

2. THE AOSERP STUDY AREA

Descriptions of geology, physiography, topography, drainage,and climate were taken from the following publications: "Atlas of Alberta" (Government of Alberta 1969), "Alberta-A Natural History" (Hardy 1967), Lombard North (1974), Carrigy and Kramers (1973), and Turchenek and Lindsay (1978).

2.1 GEOLOGY AND PHYSIOGRAPHY

The AOSERP study area covers approximately 28 000 km^2 in northeastern Alberta (Figure 1). Most of the area is underlain by Cretaceous sandstones and shales. Devonian limestone, dolomite, and gypsum are found in the northeast portion, with some Precambrian granite in the extreme northeast. Surficial deposits include till, lacustrine silts and clays, and fluvial, lacustrine, and eolian sands and gravels.

The AOSERP study area contains four physiographic regions divided into nine physiographic areas (Figure 2). The Saskatchewan Plain includes the Muskeg Mountain Upland, composed of sands and gravels over upper Cretaceous shales and sandstones, the Methy Portage and Firebag Plains, with sands and gravels over lower Cretaceous shales and sandstones, and the Clearwater Lowland, which has varved deposits overlying Cretaceous shales and sandstones. The Alberta High Plain is represented by the Stony Mountain and Birch Mountain Uplands, consisting of ground and hummocky moraines (the former with some sands and gravels) over upper Cretaceous sandstone and shale; and by the Algar Plain, consisting of sands and gravels over lower Cretaceous shales and sandstones. The Great Slave Plain contains the Athabasca Delta Plain, characterized by lacustrine deposits over Devonian limestone, dolomite,and gypsum. Granites of the Precambrian Shield are overlain by sands and gravels of the Athabasca Plain.

2.2 TOPOGRAPHY AND DRAINAGE

The AOSERP study area contains four highland areas and the Athabasca River Valley. The northward-draining Athabasca

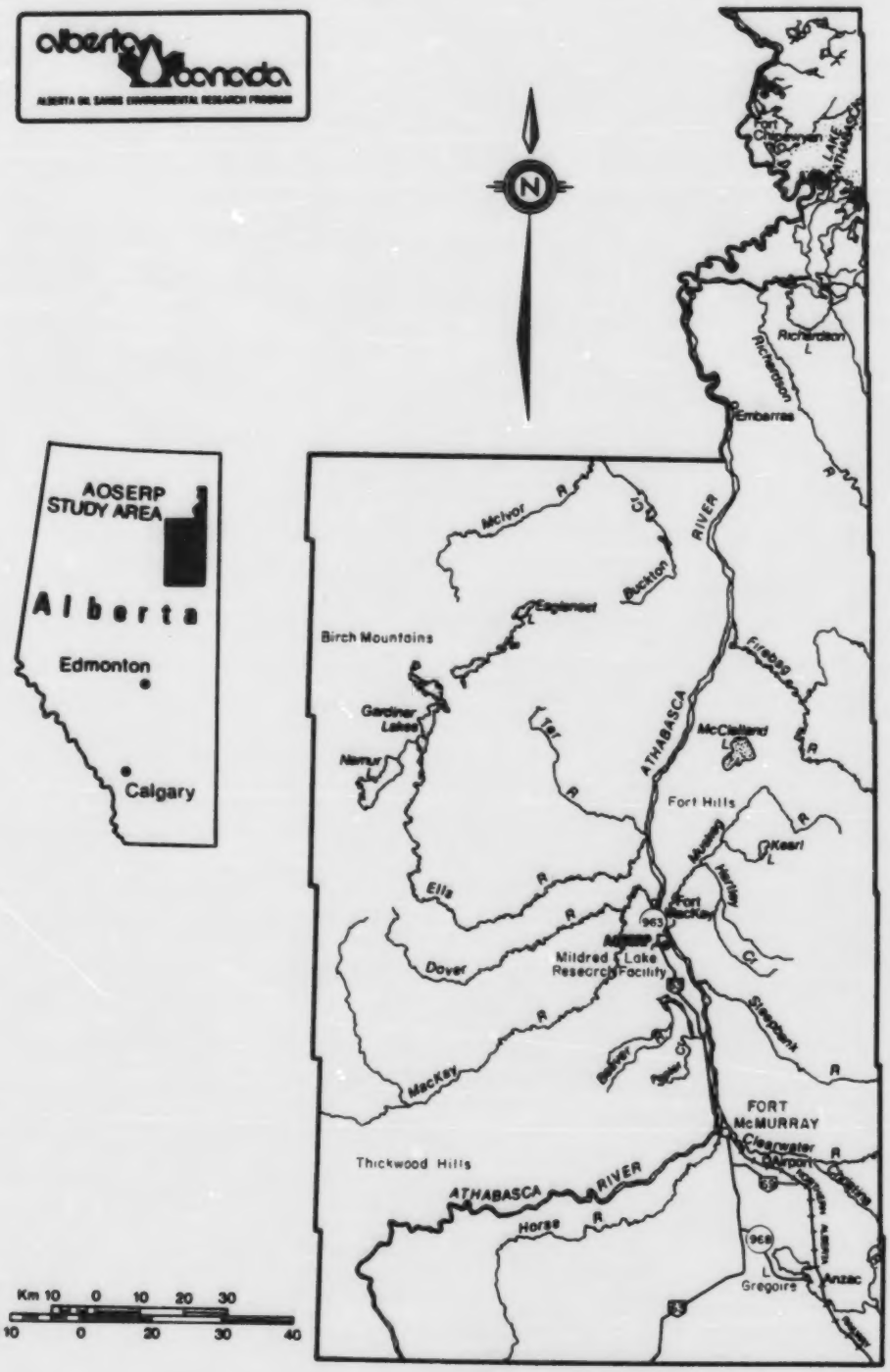

Figure 1. Alberta Oil Sands Environmental Research Program study area.

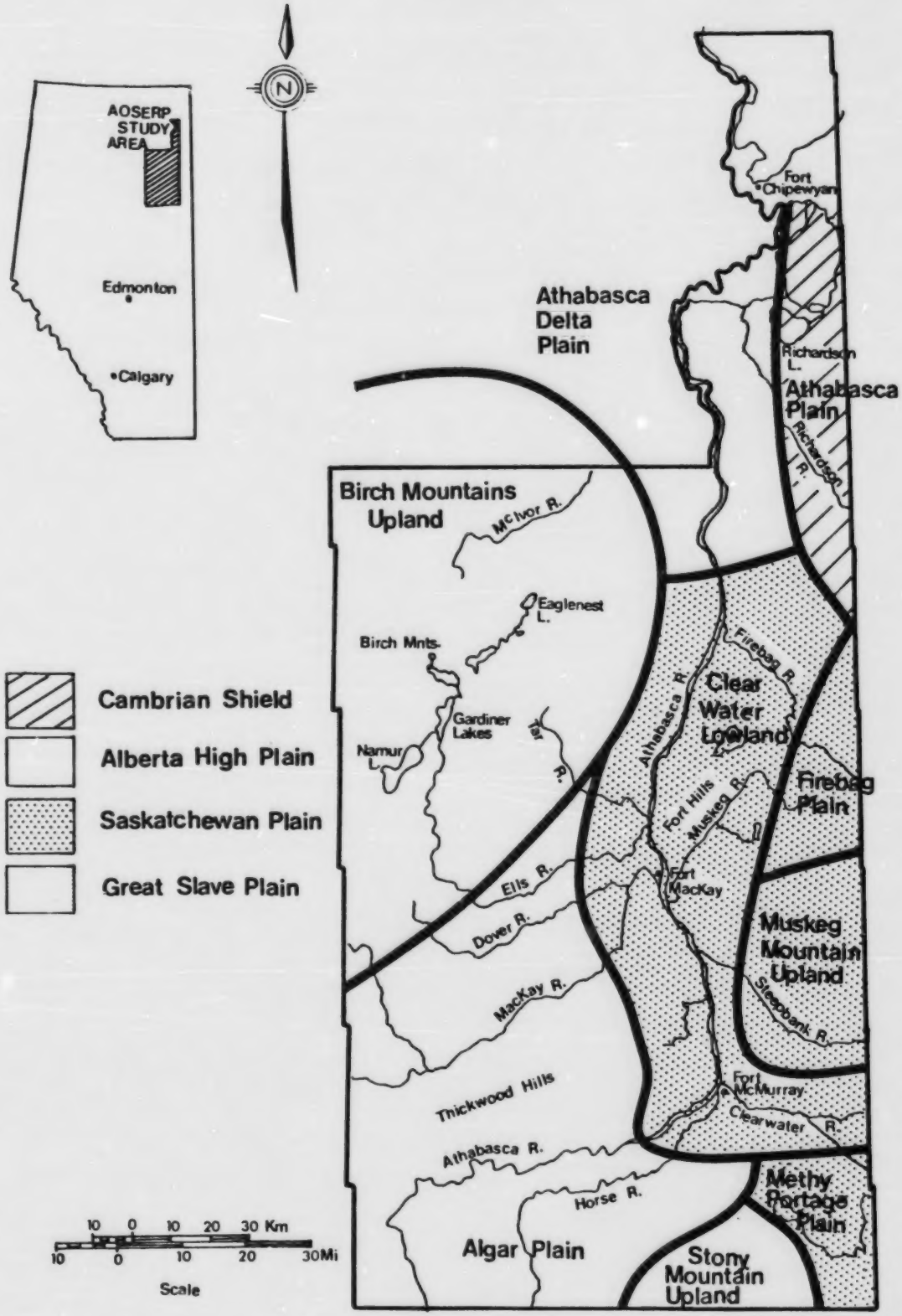

Figure 2. Physiography of the AOSERP study area (adapted from Thompson et al. 1978).

valley is 200 to 280 m above sea level. The bottom is typically covered by sandy to gravelly alluvium. The valley upstream from the Clearwater River is narrow and steep-sided and contains numerous rapids. The westward flowing Clearwater River is comparatively slow moving and meanders through a relatively broad valley bottom. In addition to the Clearwater River, a number of tributaries originate in the highland areas.

The Stony Mountains south of Fort McMurray rise gradually to 500 m and then more abruptly to about 760 m. The Thickwood Hills, west of Fort McMurray and north of the Athabasca River, gradually rise to 520 m. The Muskeg Mountains, north of the Clearwater River, rise to 580 m east of Fort MacKay before gradually sloping down to the Athabasca and Firebag rivers. The Birch Mountains, located west of the Athabasca River and north of the Thickwood Hills, gradually rise to 360 m and then rise steeply to 820 m.

The remainder of the AOSERP study area includes flat or undulating plateaus dissected and eroded in many places by steep-banked streams. There is a considerable amount of low-lying terrain consisting of bogs, fens, and muskeg. A large number of small- to medium-sized lakes are present in the Birch Mountains and northeast of the Stony Mountains. A profusion of small lakes occurs southeast of the Athabasca River Delta.

2.3 CLIMATE

The climate of the AOSERP study area is continental, with long, cold winters and short, cool summers. Mean January temperature ranges from -20°C in the south to -23°C in the north; mean July temperature is 15°C at higher elevations and 17°C in lowland areas. Winter temperatures above 5°C occur 4 to 5 days per year, and summer temperatures above 27°C average 20 days a year. Recorded temperature extremes are -55°C and 37°C. The last spring frost usually occurs between 1 June and 15 June, depending on elevation, and the first fall frost usually occurs during the

first 2 weeks of September. The growing season lasts 80 to 100 days, depending on elevation and location.

Annual precipitation ranges from about 400 mm in the north at low elevations to about 560 mm in the south at higher elevations. The average July precipitation at Fort McMurray is 75 mm with approximately 55 mm during both June and August. Snowfall averages 150 to 200 cm or more at higher elevations. Average potential evapotranspiration ranges from 350 to 500 mm, with the lower values occurring at higher elevations and latitudes. These values indicate that sufficient moisture is usually available for good plant growth except for soils with limited storage capacity such as sands, gravels, or very rocky soils.

2.4 PREVIOUS VEGETATION STUDIES IN THE REGION

There is very little in the literature that deals specifically with the vegetation of the AOSERP study area; however, a number of publications discuss the vegetation of surrounding areas.

Most of the AOSERP study area falls within Rowe's (1972) Mixedwood Section of the boreal forest. Kabzems et al. (1976) described the forest ecosystems of the Saskatchewan portion of this section. Raup (1946) included some historical review of early descriptions of the Athabasca and Clearwater rivers region and described the forests along the Athabasca River from Fort McMurray north about 80 km. Lewis et al. (1928) presented a detailed account of swamp, moor, and bog forests of central Alberta but with little locational information. Raup (1935) conducted a fairly detailed botanical investigation of Wood Buffalo National Park and designated a number of associations; he also catalogued the vascular plants of the Lake Athabasca-Great Slave Lake region northwest of the AOSERP study area (Raup 1936). Moss (1953a, 1953b) discussed associations and species of marsh and bog vegetation and forest communities west of the AOSERP study area in some detail. Moss (1932) and Duffy (1964, 1965) also discussed in detail the vegetation of the mixedwoods south of the area. Hansen

(1952) briefly discussed the postglacial forests in the Grande Prairie-Lesser Slave Lake region and speculated on their development. Lacate et al. (1965) described in detail the forests of the Lower Peace River in Wood Buffalo National Park from the standpoint of site, vegetation, and productivity. Moss (1955) provided a general treatment of the principal vegetation types of Alberta. La Roi (1967a) studied white and black spruce stands across Canada, and although no stands were located in the AOSERP study area, the paper contains considerable detail on their floristics. Achuff (1974) studied floristics and community structure of spruce-fir forests in the highlands of northern Alberta. Several of his stands were near the southern boundary of the AOSERP study area. Jeglum (1968, 1971, 1972, 1973) studied the wetlands and Swan and Dix (1966) and Dix and Swan (1971) studied the upland forest at Candle Lake, Saskatchewan, south and east of the AOSERP study area.

The Peace-Athabasca Delta wetlands and lowlands have been studied in some depth by Dabbs (1971), Dirschl (1973), and Dirschl et al. (1974). Part of this delta occurs in the extreme northern portion of the AOSERP study area.

More recently, detailed vegetation studies have been carried out in the AOSERP study area. These AOSERP-sponsored studies include those of Stringer (1976) and Thompson et al. (1978). Stringer (1976) conducted the most detailed assessment. He selected 84 homogeneous stands, each of which represented a clearly defined and undisturbed vegetation type. Stringer (1976) calculated a coefficient of similarity for all possible stand pairs based on a modified Braun-Blanquet (1965) abundance scale rating for all species except trees and rare or uncommon species. Using cluster analysis (Carmichael et al. 1968), he differentiated 10 major vegetation types and a number of other minor types, but he felt that, given a more detailed study, some of his clusters very likely could be separated into more than one type.

Thompson et al. (1978) briefly discussed the characteristic species of those vegetation types used in preparation of ecological habitat maps from aerial photographs. They purposely relied heavily on Stringer's (1976) types, although they used somewhat different type names.

Some of the leases within the AOSERP study area have been studied. Syncrude (1973) described 12 basic types on Lease 17 south of Fort MacKay, but emphasis was on wildlife habitat rather than vegetation. Peterson and Levinsohn (1977) subsequently described eight vegetation types based on dominant species on the west half of this lease and estimated forest productivity. Lombard North (1974) briefly described 11 principal plant communities on the Amoco lease in the Gregoire Lake area.

3. VEGETATION OF THE AOSERP STUDY AREA

The AOSERP study area falls completely within the Boreal Forest Region (Rowe 1972) and includes four of his Forest Sections, although the Northwestern Transition Section enters only at the extreme northeastern tip. The Mixedwood Section makes up about 75% of the AOSERP study area including the half from about Fort MacKay south and the northwestern quarter west of the Athabasca River. A small portion east of Fort MacKay falls within the Athabasca South Section but most of the northeastern quarter falls within the Upper Mackenzie Section.

Although the AOSERP study area lies completely within the Boreal Forest Region, it interacts with three other regions: the Subalpine Forest Region to the west, the Grassland to the south, and the Subarctic to the north.

The vegetation of the AOSERP study area is highly dynamic and disturbance by fire is the major influence. Vast upland areas have been burned and are in early stages of succession. The lowlands burn less frequently, perhaps only occasionally. Varying amounts of disturbance also occur in conjunction with normal stream and erosion processes. Although they rarely disturb very large areas, these processes may have important consequences for wildlife. Other areas are naturally disturbed by landslides and windfall. Most recently, man has been a major new source of disturbance.

The overall appearance of the vegetation is one of a mosaic of types, the patterns varying in extent and shape, often with lines between types being irregular, clear, and distinct.

This section covers 20 important species growing in the AOSERP study area and describes their role in the vegetation patterns observed. The species were selected following consultations with AOSERP personnel. They include the eight principal trees (aspen, *Populus tremuloides*; jack pine, *Pinus banksiana*; balsam poplar, *Populus balsamifera*; paper birch, *Betula papyrifera*; white spruce, *Picea glauca*; black spruce, *Picea mariana*; tamarack, *Larix*

laricina; and balsam fir, *Abies balsamea*); six tall shrubs (*Alnus tenuifolia, A. crispa, Salix bebbiana, Prunus pensylvanica, Amelanchier alnifolia,* and *Corylus cornuta*); two prostrate shrubs (*Arctostaphylos uva-ursi* and *Vaccinium vitis-idaea*); and four herbs (*Pyrola asarifolia, P. secunda, Aralia nudicaulis,* and *Lathyrus ochroleucus*). For each, a brief summary is given of the range, nutrient and light requirements or tolerances, role in recovery after fire, and sensitivity to sulphur dioxide (SO_2). Also described is the characteristic understory for trees and the role in the understory for the other species.

3.1 IMPORTANT TREE SPECIES AND STANDS

3.1.1 Aspen (*Populus tremuloides*)

Aspen or trembling aspen is the most widely distributed tree in North America, growing much further south than the other important trees of the study area (Figure 3). It thus grows in a wide variety of climatic conditions, ranging from the mild humid maritime climate of the Atlantic coast, where the mean January temperature is about -7°C and annual precipitation over 1000 mm, to the dry, cold, continental climate of northern Canada and interior Alaska, where the mean January temperature is about -30°C and annual precipitation 200 mm or less (Fowells 1965).

Over most of its range, aspen is usually a small- to medium-sized, fast-growing tree (12 to 18 m tall, 20 to 25 cm in diameter). Trees as tall as 30 m, 90 cm in diameter (Hosie 1973), or up to 200 years of age, however, have been recorded (Fowells 1965).

Aspen are unisexual, flowering in early spring before the leaves develop. Pollination is by wind and the fruits ripen in 4 to 6 weeks. About 5.5 to 6.6 million seeds weigh 1 kg. Dispersal is by wind or water. Seed viability is high but normally it only lasts 2 to 3 weeks. Germination is immediate, but seedlings grow slowly at first and are highly susceptible to heat,

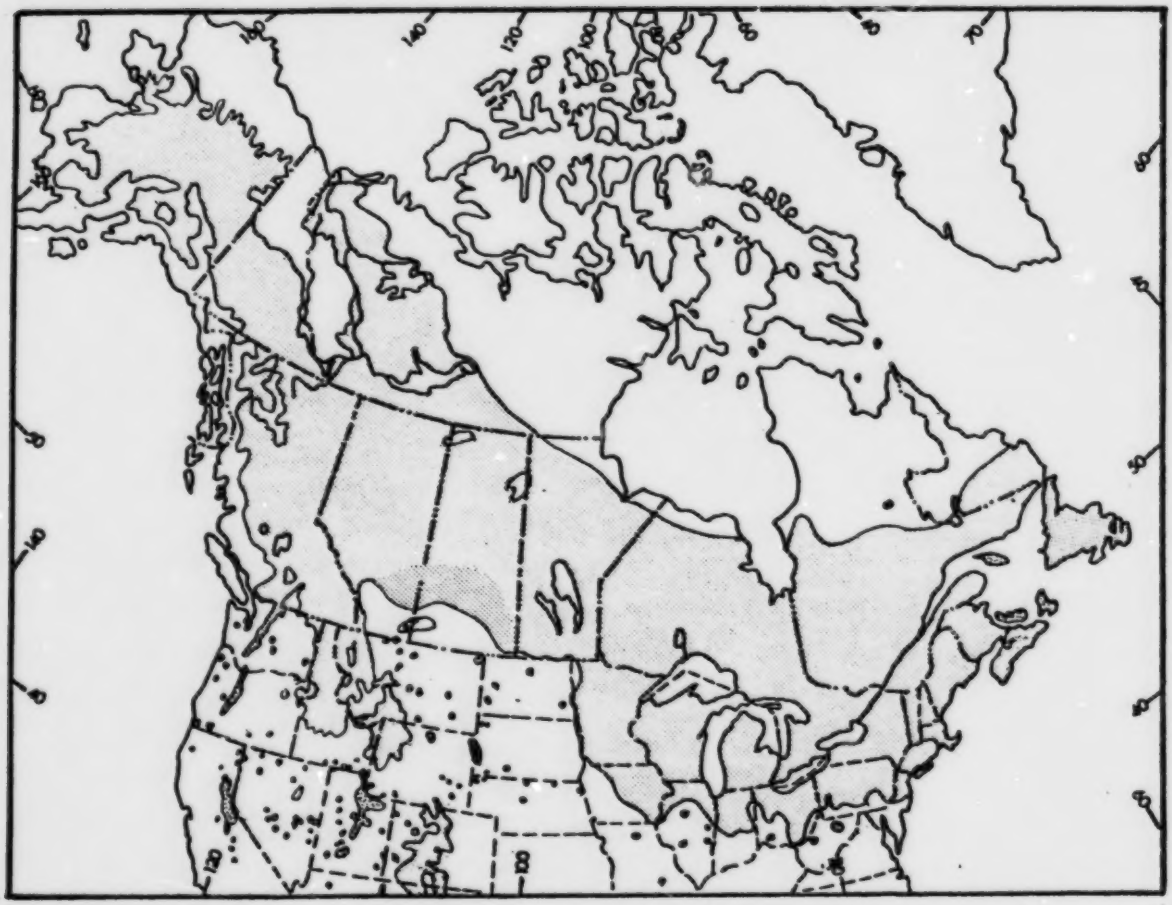

Figure 3. The range of aspen (adapted from Fowells 1965; Hosie 1973).

drought, and fungi (Fowells 1965). Although reproduction by seed generally appears to be relatively rare (Kemperman and Barnes 1976), successful seedlings can be 30 cm tall with 15 to 20 cm deep tap roots by the end of the first year. Saplings grow rapidly for the first 20 years. Thinning is rapid because aspen has a high shade intolerance. Aspen reproduces vigorously by root suckers (Fowells 1965). As a result, many individual stems are short-lived but clones can be a long-term component of the habitat (Barnes 1966).

Aspen grows on a variety of soil conditions. In central Saskatchewan, the best development is on neutral loam soils, but the species was found to be well-adapted to a wide range of soil pH and soil textures (Dix and Swan 1971) including clay soils (Moss 1955). Its best development in central Canada occurs on glacial drift rich in lime and its poorest development was on sandy and clay soils, primarily because of low nutrient and moisture conditions on the former and poor aeration on the latter. Good supplies of calcium, magnesium, potassium, and nitrogen are needed (Stoeckeler 1960; Voigt et al. 1957). Fowells (1965) felt that moisture conditions are favourable if groundwater levels are 45 to 150 cm below the surface.

Aspen produces a proliferation of root suckers when stimulated by the removal or destruction of the crown by fire. Aspen requires a high light intensity; saplings or seedlings do not survive under heavy shading for more than 1 or 2 years (Shirley 1941). Thus, its successful regeneration or establishment is restricted to early stages of recovery after disturbances (Halliday and Brown 1943). Moss (1953b, 1955) noted that while fire, particularly severe fire, has a devastating effect on spruce, it causes only a temporary setback to aspen because of its root-suckering ability. On well-drained alluvial lowlands of the lower Peace River, aspen often recovered in almost pure stands and was usually a major component on slopes and uplands, tending to replace jack pine on areas with numerous light burns (Lacate et

al. 1965). Northwest of the Peace River, aspen also invaded sandy sandy prairie areas by suckers (Jeffrey 1961). Raup (1946) considered aspen to be an important early successional tree in Wood Buffalo National Park, particularly on upland areas and some well-drained lowlands.

In addition to competition and shade intolerance, numerous other natural factors injure or kill aspen. Saplings are often heavily browsed by numerous mammals including rodents, hares, deer, and moose. The fungi of greatest economic significance are the wood-rotting fungi and the cankers, and the most important insect enemies are the poplar borer and the forest tent caterpillar.

Trembling aspen is quite sensitive to SO_2. It is more sensitive than jack pine, white birch, tamarack, balsam poplar, or white spruce (Dreisinger and McGovern 1970, cited by Loman et al. 1972 and Loman 1975). Visible foliar injury results from exposure to about 0.13 ppm for 8 h, 0.2 ppm for 5.5 h, 0.3 ppm for 3 h, or 0.4 ppm for about 1 h. For most exposures, this is only 0.05 to 0.08 ppm above the maximum acceptable SO_2 level (Loman 1975). Karnosky (1976), however, reported clonal variation in sensitivity to SO_2. Threshold levels for foliar injury after 3 h of exposure ranged from 0.35 to 0.65 ppm of SO_2 and 0.05 to 0.20 ppm of ozone. Much of that colonal variation was attributed to genetic differences (Karnosky 1977). Exposing aspen to a mixture of SO_2 and NO_2 did not result in greater-than-additive effects (Reinert et al. 1975) but such effects result from combined exposures to SO_2 and ozone (Karnosky 1976).

An iron sintering plant at Wawa, Ontario, emitting 90 000 t of "sulphur" per year for 11 years, significantly affected downwind boreal forest vegetation (Gordon and Gorham 1963). Trembling aspen trees were only present 25 km or more from the plant and showed tip kill and crown thinning to a distance of at least 32 km. Aspen seedlings were present from 27 km out. Damage conditions do not appear to have stabilized and the areas affected were expanding (Gordon and Gorham 1963).

Pollutants are believed to stress plants and make them more susceptible to infection by microbial pathogens, but more often the reverse is true. For aspen, parasitic fungi generally appeared to be retarded or inhibited where SO_2 was present. Two rusts were absent in the area of greatest SO_2 injury but occurred sparsely where injury was moderate and abundant where injury was least (Treshow 1975).

Aspen is suspected to have several climatic races, two of which are probably classed as varieties. Natural hybrids with *Populus grandidentata* and the European *P. alba* are known to produce fertile viable seed and numerous other artificial crosses are reported (Fowells 1965; Maini and Cayford 1968). The population of hybrid poplars in Alberta appears more extensive and complex than had been suspected (Brayshaw 1965).

Aspen is generally used for pulpwood. Occasionally, lumber is cut for boxes, crates, excelsior, and matches, and selected logs are used for veneer and plywood (Maini and Cayford 1968; Hosie 1973). Current usage of "poplar" (*Populus* spp.) in Canada was pulpwood (55%), plywood (15%), particle-board (13%), lumber (8%), and export (9%) (Armson and Smith 1978). Total volume of aspen on mature stands of the Mixedwood Section of Saskatchewan varies from 140 m^3/ha for marginally commercial stands on very rapidly and rapidly drained sites to 210 m^3/ha on well-drained sites and over 315 m^3/ha on the best moderately well-drained sites (Kabzems et al. 1976). Peterson and Levinsohn (1977), however, only reported gross volumes of 72 to 195 m^3/ha for mixed aspen-white spruce stands on the west half of Syncrude Lease 17.

Numerous understory species occur in aspen stands. Stand composition varies with site characteristics, and as a result of such chance factors as season of disturbance, species availability for recolonization, and type and severity of disturbance. Stringer (1976) classified aspen-dominated sites in the AOSERP study area as Upland and Mixedwood Deciduous Forest. Peterson and Levinsohn (1977) described a floristically similar type (their aspen-white spruce type) covering about 26% of the west half of Syncrude Lease 17 southwest of Fort MacKay.

Stringer (1976) found *Alnus crispa* was common and contributed considerable cover in the tall shrub layer. In the medium shrub layer, *Vaccinium myrtilloides*, *Viburnum edule*, and *Rosa acicularis* were the major components, with *Ledum groenlandicum*, *Symphoricarpos albus*, *Shepherdia canadensis*, and *Ribes triste* often present. The herb-low shrub layer was variable with *Linnaea borealis*, *Cornus canadensis*, *Petasites palmatus*, *Mitella nuda*, *Epilobium angustifolium*, and *Vaccinium vitis-idaea* most consistently important. Others usually included *Schizachne purpurascens*, *Lycopodium* spp., *Galium boreale*, *Maianthemum canadense*, *Fragaria* spp., and *Lathyrus ochroleucus*. *Calamagrostis canadensis* and *Elymus innovatus* were two grasses usually present but they seldom made up more than 5% of the groundcover.

Moss (1955) also included as typical species *Rosa woodsii*, *Rubus* spp., *Corylus cornuta*, and *Salix* spp. in the shrub layer and *Aster ciliolatus*, *Vicia americana*, *Pyrola* spp., *Viola rugulosa*, *Thalictrum venulosum*, *Agropyron trachycaulum*, and *Aralia nudicaulis* in the herbaceous stratum. A total of 133 vascular plants and 26 bryophytes and lichens were reported in 20 stands in northwestern Alberta (Moss 1953b). Several mosses, including *Pleurozium schreberi* and *Hylocomium splendens*, were almost always present, seldom covering much of the ground. Kabzems et al. (1976) listed similar species in a variety of combinations for aspen-hazelnut types of the Mixedwood Section of Saskatchewan.

Peterson and Levinsohn (1977) described an aspen-birch type on recent burns. This type was not sampled by Stringer (1976) since his study focussed on mature forests. Major understory, tall shrubs in the aspen-birch type include juvenile aspen, poplar, willows, *Alnus crispa*, and on some sites *Shepherdia canadensis*. Present in lesser amounts are *Lonicera dioica*, *Cornus stolenifera*, *Ribes oxyacanthoides*, *Betula pumila*, and *Lonicera involucrata*. Lower shrubs include *Ledum groenlandicum* and *Vaccinium myrtilloides*. The dwarf shrub-herb layer was highly variable.

3.1.2 Jack Pine (*Pinus banksiana*)

The other species common on recently burned areas is jack pine. It is principally a tree of the boreal forest region but extends from Nova Scotia and New England across the northern half of the prairies to the central Mackenzie Valley (Figure 4). It grows the farthest north of the North American pines.

Although it grows near the Atlantic coast, it is more common in a continental climate. Mean January temperatures range from -29° in the northwest to -4°C in the southwest and mean July temperatures from 13 to 22°C. Mean annual precipitation ranges from 250 to 1300 mm but 380 to 890 mm are more common (Fowells 1965).

Jack pine is generally a short-lived conifer, with stands on the best sites deteriorating after 80 to 100 years; it is small-to-medium in size, growing 12 to 18 m tall and 20 to 30 cm in diameter, although trees up to 24 m tall and 60 cm in diameter are known (Hosie 1973).

Male cones develop largely on the basal part of the new shoots of older lateral branches, and femal cones at the tip of the main shoot. Flowering occurs in May to June, and the cones ripen 15 months later. Seed production normally starts at age 5 to 10 for trees growing in the open and 10 to 25 for trees in stands, but production is best in 40 to 50 year old trees. Good seed crops are produced every 3 to 4 years, with light crops in intervening years. Jack pine cones are largely serotinous, requiring heat to open, except in trees along the southern edge of the range, or where ifre is infrequent. Released seed usually germinates within a few weeks and seedling establishment is best where there is some shade. Seedling growth is slow at first, but by the fourth year, seedlings can be 30 to 90 cm tall. On the study area, jack pine is the fastest growing conifer other than tamarack during the first 20 years. Jack pine normally does not reproduce vegetatively (Fowells 1965).

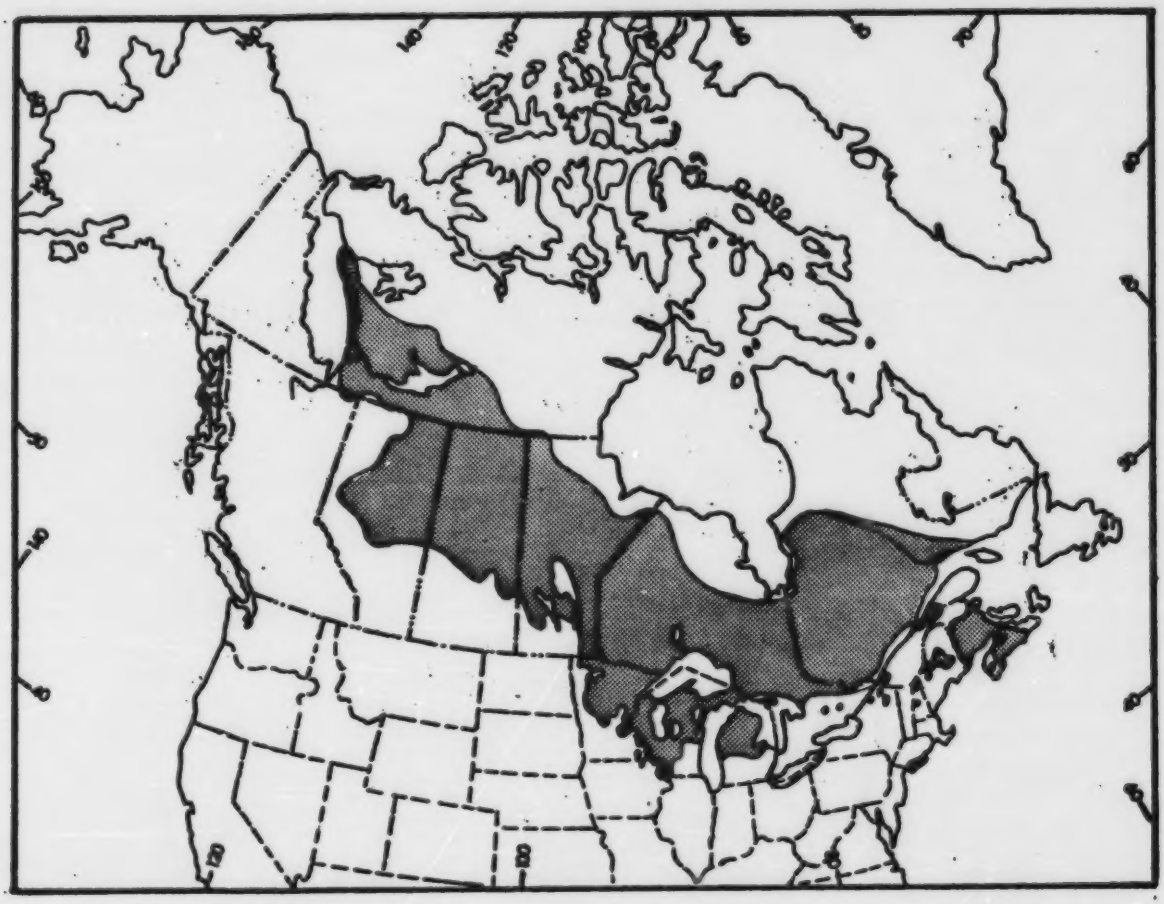

Figure 4. The range of jack pine (adapted from Fowells 1965; Hosie 1973).

Dix and Swan (1971) considered it a pioneer species on sand and sandy loams, primarily on dry sites. Jack pine usually occurs on sandy and gravelly soils on hills and ridges in northwestern Alberta, but occurs increasingly on heavier soils as one moves westward (Moss 1953b). It is predominant on sandy plains and rocky hills in the Athabasca-Great Slave Lake area, but it also grows on a variety of sites ranging from extremely xeric sites such as dunes to the very wet margins of ponds and lakes (Raup 1946). In the Mixedwood Section of Saskatchewan, jack pine stands are prevalent on very rapidly and rapidly drained sand, loamy sand, and gravel soils developed on glaciofluvial, fluvial, lacustrine, or aeolian deposits (Kabzems et al. 1976).

Jack pine has a strong tendency to develop a tap root, giving it a competitive edge in sandy and gravelly soils where it can penetrate to moisture (Moss 1953b). The tap root, however, does not give it a competitive advantage in heavy soils which are not readily penetrated (Sterrett 1920).

Jack pine occurred on sites with a wide range of pH but showed a preference for acid conditions in Saskatchewan (Dix and Swan 1971). It could grow on soils with a pH as high as 8.2, however, if sufficient mycorrhizal development was present (Dale et al. 1955).

Jack pine is well adapted to its role as a pioneer species, particularly after fire: in fact, it appears to be a highly flammable, fire dependent species. This flammability might seem a contradictory attribute for a fire-adapted species, but Mutch (1970) postulated that natural selection has favoured development of highly flammable characteristics of many fire-adapted species in a number of vegetation types throughout the world. Rapid, intense burning on a relatively frequent basis insures their perpetuation.

The best adaptation of jack pine to fire is the presence of serotinous cones which normally open slowly or not at all until heat is applied. Fires which briefly reach a temperature of

several hundred degrees will open the cones without damaging the seed, unless the cone actually burns (Eyre 1938; Eyre and LeBarron 1944). Jack pine cones can tolerate up to 480°C for 30 sec and 370°C for 3 min; seeds survive 370°C for 10 to 15 sec (Beaufait 1960). Seeds in a closed cone can remain viable for at least 15 years (Roe 1963) and are retained on the tree for several years.

Jack pine seed from a burned tree may germinate within 4 days of artificial seeding (Fowells 1965). Germination on a cut-over area in Minnesota was 60% on mineral soil, 47% on scarified duff, 49% on burned duff, but only 17% on undisturbed duff (LeBarron 1944). Seedlings cannot establish themselves if the organic layer is not burned to within 1.25 cm of the mineral soil, but Ahlgren (1959) found that good seedling establishment occurred in Minnesota when the organic layer was reduced to 2.5 to 5.0 cm, but virtually none occurred if 7.5 cm or more were present. In Ontario, however, a strong curvilinear relationship exists between jack pine frequency and depth of humus after fire (Chrosciewicz 1974). The best seed beds had 0.5 cm or less humus and low germination resulted if humus depth exceeded 3.8 cm.

Two of the more important habitat factors affecting seedling establishment are moisture and weather conditions. In a Manitoba seeding trial, jack pine was much easier to establish than either white or black spruce and developed a much larger root system (Jarvis 1966). This presumably increases survival in areas subject to surface drying such as after burning.

Jack pine is attacked by a variety of pests and enemies in its life cycle. Seeds are eaten by many kinds of birds and rodents, and several insect pests can kill up to 25% of seedlings; fungal infections and high populations of deer or hare can similarly kill large numbers of seedlings. Mature trees are also susceptible to a great variety of fungal and insect pests but porcupines appear to be the only major animal pest (Fowells 1965).

Jack pine is judged more sensitive to SO_2 than white spruce or balsam poplar but less than trembling aspen. Visible foliar injury results from exposures to SO_2 levels of 0.2 ppm for 8 h, 0.3 ppm for about 4.5 h, 0.4 ppm for about 2.5 h, or 0.5 ppm for 1 h. These levels are about 0.07 to 0.1 ppm higher than that required for similar effects on aspen and 0.1 to 0.15 ppm above the "maximum acceptable" level (Dreisinger and McGovern 1970, cited by Loman 1975). Downwind of the iron sintering plant near Wawa, Ontario, which emitted 90 000 t of "sulphur" per year for 11 years, jack pine trees were only present 25 km or more from the plant, but many were reddened and some chlorotic. Jack pine seedlings were only present from 25 km out (Gordon and Gorham 1963).

In addition to SO_2, jack pine is sensitive to ozone and related oxidants; they cause emergence tip burn. Jack pine (along with white pine) may serve as one of the best early indicators of chronic ozone injury (Miller and McBride 1975).

Jack pine grows over a wide geographic area and has developed considerable genetic diversity. Serotiny shows a gradual change from a closed cone type in the north to an open cone type in the south; at least four ecotypes are suspected in the Lake States. In Alberta, the ranges of jack pine and lodgepole pine (*Pinus contorta*) overlap and natural hybrids are known (Moss 1949; Yeatman 1967, 1974). Also reported is an artificial hybrid with Scotch pine (*P. sylvestris*) (Fowells 1965).

Jack pine is used for general construction and for pulp. It takes creosote well and is used for railway ties, poles, pilings, fence posts, and mine timbers (Hosie 1973; Yeatman 1974; Kabzems et al. 1976).

Productivity data for jack pine stands are available for the Saskatchewan portion of the Mixedwood Section (Kabzems et al. 1976). Yields vary with site conditions. On very rapidly and rapidly drained sites with coarse textured soils, mature stands of pure jack pine produce about 90 m^3 of merchantable volume per hectare. On well-drained sites, stands with about 90%

jack pine and 10% combined aspen, poplar, and black and white spruce tree cover, yields are 130 to 140 m^3/ha at a 70 year rotation but increase to 180 m^3/ha at maturity (100 to 110 years of age). The best growth is on moderately well-drained sites. Jack pine dominated stands on such sites have about 70% jack pine cover; the remainder consists largely of aspen, white spruce, and black spruce. Yields at 60 to 65 year rotation are 170 to 190 m^3/ha but at maturity (90 to 100 years) yields are 260 to 275 m^3/ha. Some imperfectly drained sites support mixed jack pine-black spruce stands (60 and 40%, respectively). Total yields are 105 to 140 m^3/ha at a 75 year rotation age. Yields can be increased by selective harvesting, thinning, favouring growth of the better trees, and possibly fertilization (Armson 1978).

Floristically, jack pine stands may be the simplest of the boreal forest types. Raup (1946) found only six vascular species over large areas and sometimes over "many acres" jack pine was the only vascular species present. Frequency data presented by Dix and Swan (1971) support the floristic simplicity of jack pine stands at Candle Lake, Saskatchewan; however, stands of balsam fir and, to a lesser extent, white spruce appeared to be at least as impoverished.

Two phases of jack pine stands grow in Wood Buffalo National Park--stands on sandy plains and ridges and stands on rocky hill sites (Moss 1953b, 1955; Raup 1946). Raup (1946) stated that "primary" species on both types were *Arctostaphylos uva-ursi* and the lichens *Cetraria nivalis* and *Cladina rangiferina*. In his rocky hill sites, additional "primary" species were *Amelanchier alnifolia*, *Saxifraga tricuspidata*, and *Artemisa frigida*, and in sandy woods, *Alnus crispa*, *Vaccinium myrtilloides*, and *V. vitis-idaea*.

Two floristic jack pine stand types apparently also exist in the AOSERP study area, depending on whether jack pine is the lone dominant or shares dominance with another tree species

(Stringer 1976). *Vaccinium vitis-idaea, V. myrtilloides,* and the lichen *Cladina mitis* were important and abundant species in both types. *Cladina alpestris, Cetraria nivalis, Peltigera malacea,* and *Cladonia uncialis,* though common, did not afford much ground cover. Species apparently limited to stands where jack pine is the single dominant included *Arctostaphylos uva-ursi, Oryzopsis pungens, Campanula rotundifolia, Apocynum androsaemifolium, Solidago nemoralis,* and *Maianthemum canadense.*

In stands where dominance was shared with another tree species, the understory, although variable, contained several characteristic species. Important tall shrubs were *Salix bebbiana* and, to a lesser extent, *Alnus crispa.* The most consistently important understory species was *Ledum groenlandicum,* with *Elymus innovatus* and *Cornus canadensis* usually contributing relatively large amounts of cover. Mosses which were common and nearly covered the ground include *Pleurozium schreberi, Hylocomium splendens,* and *Polytrichum juniperinum,* along with the lichen *Peltigera aphthosa.* Similar types are found in the Mixedwoods Section of Saskatchewan on well-drained sites (Kabzems et al. 1976). Stringer's report did not include site descriptions, and more comparison with Raup's (1946) findings is not possible.

At Candle Lake, Saskatchewan, Dix and Swan (1971) evaluated relative species frequencies under the various crown cover types and grouped species according to three classes of specificity for canopy type. Although difficult to compare directly with Stringer's (1976) results, there are similarities. One major exception is that Dix and Swan (1971) found *Vaccinium vitis-idaea* to be highly specific for jack pine canopy, but cover-abundance values determined by Stringer (1976) do not completely agree. They considered *Arctostaphylos uva-ursi* to have only an intermediate specificity for canopy type; however, on the AOSERP study area, it contributed significant cover, primarily under jack pine dominated canopies. No other comparisons were made because frequency values may be misleading when attempting to assess what

they mean in terms of a species influence on the community. In addition, Stringer (1976) sampled relatively few stands of jack pine, which may mean his findings are not typical of the whole AOSERP study area.

3.1.3 Balsam Poplar (*Populus balsamifera*)

Balsam poplar is another important tree on the AOSERP study area. It is transcontinental in distribution from Newfoundland, the Maritimes, and New England, in the southeast, to Alaska, in the northwest (Figure 5).

Climatic conditions vary considerably throughout this range. Mean January temperatures range from -4 to -30°C; mean July temperatures 12 to 30°C; mean annual precipitation from 1400 to 180 mm; and the frost-free period from up to 150 days to 75 days (Fowells 1965).

Balsam poplar is a medium-sized deciduous tree, 18 to 24 m tall and 30 to 60 cm in diameter, although occasional trees are 30 m tall and 120 cm in diameter (Hosie 1973). It is short-lived in the southern part of its range, but trees up to 200 years old are known in the north (Fowells 1965).

The flowers open in early spring before the leaves appear and the seeds mature in a few weeks before the leaves are fully developed. Seeds are dispersed immediately, largely by wind. Germination must be immediate or the seed will die since seed viability lasts only a few days (Fowells 1965).

Balsam poplar is also considered to be a pioneer species in the boreal forest (Dix and Swan 1971; Rowe 1970, Raup 1935). Dix and Swan (1971) found it to be associated with a wide variety of soil textures, from sandy loams to clays (the only major species associated with clay soils), soils of pH greater than 7, and poorly to moderately drained soils. Moss (1932) found it to grow on all but the wettest soils and seldom on dry exposed sites. Soil texture is not as important as abundant moisture, and balsam poplar appears to be about as shade intolerant as aspen (Fowells 1965).

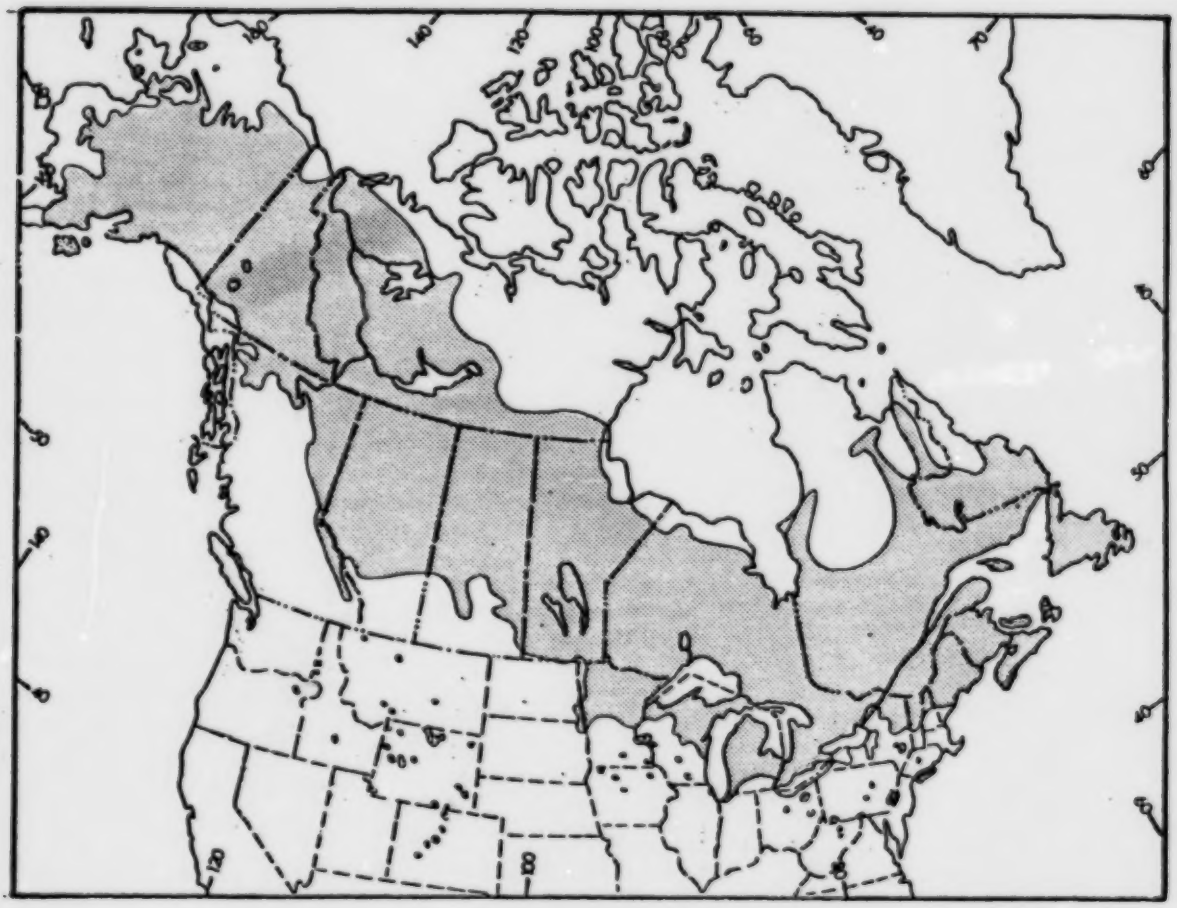

Figure 5. The range of balsam poplar (adapted from Fowells 1965; Hosie 1973).

Balsam poplar, however, is usually associated with alluvial bottoms and river flats (Moss 1955), sand bars, and stream banks and around lakes and marshes (Raup 1946), as long as its pH and moisture requirements are met. It is also a common component of mesic upland forests on the AOSERP study area (Stringer 1976) and surrounding areas (Lacate et al. 1965, Lewis and Dowding 1926).

Balsam poplar is well-adapted to its role as a pioneer species. Great quantities of seeds are reproduced almost every year and may be carried long distances by wind (Lutz 1956). These germinate immediately when seedbed conditions are favourable. Seedlings are delicate and require continuous moisture for at least a week or two (Day and Vogel 1944). These conditions occur most frequently on lowlands with recent overflow and occasionally on recently burned upland mineral soil.

Reproduction also takes place by root suckers. This may be the main mode of reproduction in Alberta (Moss 1932). In Alaska, suckering may be the restocking mechanism following fires, with the primary role of seed being invasion of new sites (Lutz 1956).

Under similar conditions, balsam poplar usually grows faster than aspen (Moss 1932) and will grow under competitive conditions only if it is dominant (Day and Vogel 1944). It outgrows aspen and birch on mesic to wet lowland sites but usually gives way to aspen and paper birch on many upland sites where they are better adapted (Fowells 1965). Aspen may, nevertheless, dominate a mesic site if it invades in advance of balsam poplar. The reverse can happen on upland sites if balsam poplar is the earliest invader. In both situations, this results from the shade intolerance of each species. In a mixture with aspen, balsam poplar eventually dominates due to its longer life span (Moss 1932).

Balsam poplar has numerous natural enemies. These include the forest tent caterpillar and wood rotting fungi, although both affect aspen to a greater extent (Fowells 1965).

Balsam poplar is less sensitive to SO_2 than jack pine or aspen but more than white spruce. Visible foliar injury results from exposures to SO_2 levels of about 0.25 ppm for 8 h, 0.4 ppm for about 5 h, 0.5 ppm for about 3.5 h, 0.6 ppm for about 2.5 h, 0.7 ppm for about 1.5 h, and 0.8 ppm for about 1 h. These values are about twice the "maximum acceptable" SO_2 levels (Dreisinger and McGovern 1970, cited by Loman 1975).

Various forms of balsam poplar grow throughout the prairies and there is extensive interbreeding with such species as *Populus trichocarpa*, which some consider as a subspecies of balsam poplar (Hosie 1973). Numerous natural hybrids and artificial crosses are reported (Brayshaw 1965; Maini and Cayford 1968).

Poplar is used in windbreaks on the prairies and the wood is used for plywood, excelsior, and pulpwood (Hosie 1973, Maini and Cayford 1968). Current usage of *Populus* spp. in Canada is pulpwood (55%), plywood (15%), particleboard (13%), lumber (8%), and export (9%) (Armson and Smith 1978). Peterson and Levinsohn (1977) reported gross volumes of 139 m^3/ha, of which 94 m^3/ha were merchantable, for balsam poplar-alder stands in the MacKay River valley of the AOSERP study area.

Stringer (1976) found practically pure stands of balsam poplar on the AOSERP study area along the Clearwater River and along portions of the Athabasca River. They probably are also locally abundant along the major tributaries. Peterson and Levinsohn (1977) reported a floristically similar type (their balsam poplar-alder type) along the MacKay River Valley.

The tall shrub layer (Stringer 1976) contained varying mixtures of *Alnus tenuifolia* and *Cornus stolonifera* overtopping occasionally dense stands of *Viburnum edule, Ribes oxyacanthoides, R. triste, Rosa acicularis,* and *Rubus strigosus. Calamagrostis canadensis,* the major grass species, was fairly abundant in most stands. *Equisetum pratense, Galium triflorum,* and *Rubus pubescens* were the most consistently important associated understory herb

and low shrub species, although numerous other species were present and often occurred abundantly on some sites. Mosses were scattered and common but not prominent. Those often covering lower trunks and tree bases included *Eurhynchium pulchellum*, *Plagiomnium cuspidatum*, and *Brachythecium salebrosum*. Others growing on organic materials on the forest floor included *Brachythechum rutabulum*, *Amblystegium juratzkanum*, *Campylium hispidulum*, *Drepanocladus uncinatus*, *Haplocladium microphyllum*, and *Oncophorus wahlenbergii*. Two mosses, *Hypnum pratense* and *Timmia megapolitana*, were only found in balsam poplar stands, with no lichens or liverworts being reported in the stands sampled (Stringer 1976).

Although Moss (1953b), Dix and Swan (1971), and Raup (1946) did not study the non-vascular flora, their vascular species lists are very similar, with somewhat different relative importances.

3.1.4 Paper Birch (*Betula papyrifera*)

Paper birch (or white birch), with its many varieties, has a transcontinental distribution (Figure 6) similar to balsam poplar. It thus experiences a similar range of climatic conditions although it is largely considered a cold-climate species, seldom growing naturally where mean July temperature exceeds 21°C It is generally a medium-sized tree 21 m tall and about 25 cm in diameter but occasionally trees grow to 30 m tall and 75 cm in diameter. A short-lived species, paper birch matures in 60 to 75 years and few trees live beyond 140, although occasional 200 year old trees are found (Fowells 1965).

Paper birch flowers in spring; the seeds ripen and are released in early fall, dispersed largely by wind. Germination takes place the following spring.

Paper birch is another component of the AOSERP study area vegetation considered to be a pioneer species (Dix and Swan 1971). At Candle Lake, it grew primarily on sandy and sandy loam soil, although it may also grow on rocky soil and even on organic

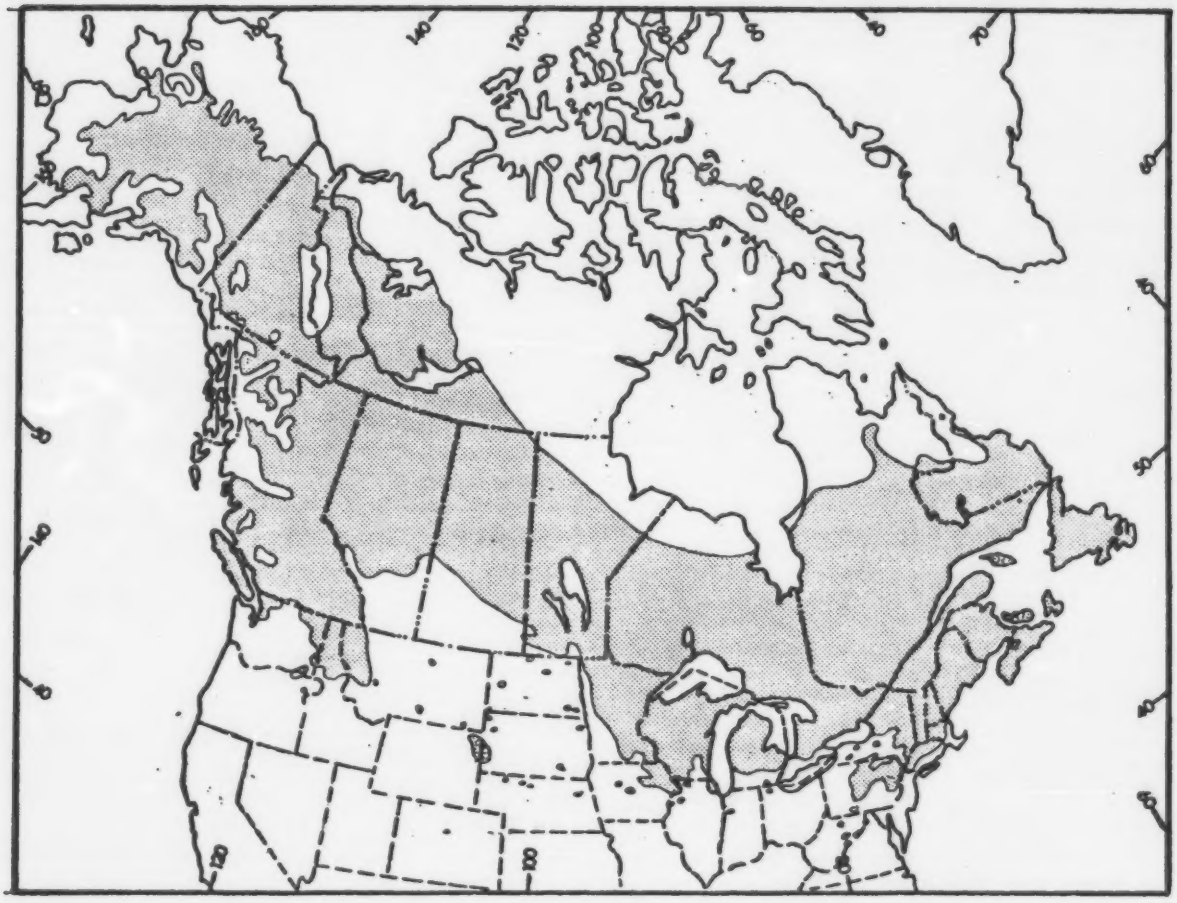

Figure 6. The range of paper birch (adapted from Fowells 1965; Hosie 1973).

soil associated with peat and bogs (Fowells 1965). Dix and Swan (1971) found paper birch stands only on soils of pH 5.3 or less, but it can also be found on highly calcareous soils (Fowells 1965). It most often occurs on dry to mesic sites (Raup 1946; Dix and Swan 1971).

Paper birch appears to be adapted to its pioneer role as it produces an abundance of very small seeds (3.3×10^6/kg), easily carried by the wind. In addition, it can reproduce by root or stump sprouts. Paper birch seeds are known to lose their viability quickly (Fowells 1965). Leaf litter is the least desirable seedbed (Hutnik 1954) since the sprouted seed cannot penetrate a leaf to reach the soil, and if it sprouts under a leaf, it succumbs because of a requirement for direct sunlight. Mineral soil and rotted wood apparently make the best seedbeds (Hutnik 1954).

Once established, seedlings grow rapidly when overhead light is available, but many die due to shade intolerance. Eventually, only those dominant individuals which later make up the mature canopy survive. Paper birch is thus rated as a species very intolerant to competition (Baker 1949), although it may be slightly more tolerant than aspen. Almost paradoxically, it appears to be self-perpetuating in stands in numerous boreal forest locations that meet the light requirements of seedlings (Buell and Niering 1957; Moss 1955; Raup 1946).

Where paper birch stands have been selectively logged and the stands opened, post-logging decadence has been observed. The symptoms are similar to those of natural birch dieback of undisturbed stands where vigour is lowered, growth reduced, and ultimately the trees die. The causal agent is unknown. Numerous insect and fungal pests may attack trees suffering dieback and hasten their death. Successive years of forest tent caterpillar infestations may greatly reduce annual growth (Fowells 1965).

Paper birch appears to be slightly less sensitive to SO_2 than aspen, and of similar tolerance to jack pine and aspen

(Dreisinger and McGovern 1970, cited by Loman et al. 1972). In Gordon and Gorham's (1963) investigations of the effects of an iron sintering plant emitting 90 000 t of "sulphur" per year for 11 years, however, only it and white spruce were still alive as close as 17 km to the plant, although they appeared to be dying. Among tree seedlings, paper birch occurred closest to the plant, from 15 km out.

Birch trees appear to be more tolerant to fluorine than spruce or fir (Miller and McBride 1975). It has also been observed that birch leaf rust was absent from birches around an aluminum plant in Norway although the disease was widespread in the region, indicating that the pathogen is more sensitive to fluorine than the host (Treshow 1975).

Numerous integrating, geographical varieties of paper birch have been named. Fowells (1965) lists six and Hosie (1973) discusses three as being distinctive in Canada. Polyploidy is very pronounced in paper birch and its varieties and hybridization is common (Brittain and Grant 1965a, 1965b, 1966, 1967).

Paper birch is an important hardwood, used for special products, turnery, veneer stock, and pulpwood (Hosie 1973). Good sites in New England will produce about 200 to 250 m^3/ha in 50 years. Similar yields have been reported in Alaska (Fowells 1965).

Understory species of paper birch stands are not much discussed in the literature. They appear to be about the same as one would expect to find in aspen and balsam poplar stands, based on Dix and Swan's (1971) frequency data and Stringer's (1976) cover-abundance data.

3.1.5 White Spruce (*Picea glauca*)

White spruce is a major component of the boreal forest. Raup (1935, 1946), Moss (1953b), and Lacate et al. (1965) considered it to be the dominant species for the general region of the AOSERP study area; however, Dix and Swan (1971) consider it to be a "chiefly pioneer" species at Candle Lake, Saskatchewan.

White spruce has a transcontinental distribution from the Atlantic coast (Maritimes, New England) on the southeast to the Bering Sea on the northwest (Figure 7). It grows in the same wide range of climatic conditions as the other boreal species with similar distribution discussed previously (e.g., aspen, balsam poplar). Trees average about 24 m in height and diameters of 60 cm, but trees up to 36.5 m tall and over 120 cm in diameter are known (Hosie 1973).

White spruce occupies a diversity of sites from clays (Wilde et al. 1954; Nienstaedt 1957) to sands and rocky soils (Rowe 1972). It may also occur on organic soils but is not characteristic of them (Rowe 1972). Dix and Swan (1971) found stands dominated by white spruce on soil textures ranging from silt to clay loam (but not on clays), with the greatest proportion occurring on loams. White spruce dominated stands will also grow in rocky crevices on bedrock where a small amount of soil had collected (Raup 1946). The best developed stands occurred on low alluvial plains along major drainageways.

White spruce tolerates a wide range of pH (Nienstaedt 1957); in stands in Saskatchewan, it grew on soils of pH 4 to 8 (Dix and Swan 1971).

White spruce will occupy dry fertile sites, but no fertile site is too moist if the water is not stagnant (Sutton 1969). It occupied mesic sites (the water table more than 60 cm below the surface) in Saskatchewan, with few stands occurring on dry sites (Dix and Swan 1971).

White spruce does not seem particularly well-suited as a "chiefly pioneer" species [Dix and Swan's (1971) classification] for several reasons. Its cones are not serotinous in nature and drop most of their seeds over a 2 month period during the growing season (Roe 1946). Cones are produced every year, but only in quantity every 2 to 6 years (Sutton 1969); in Alberta, the cycle may be 7 years (Lees 1963). In addition, the small winged seeds usually fall within 100 m of the parent tree (Rowe 1955), although they can be carried up to 300 m by wind.

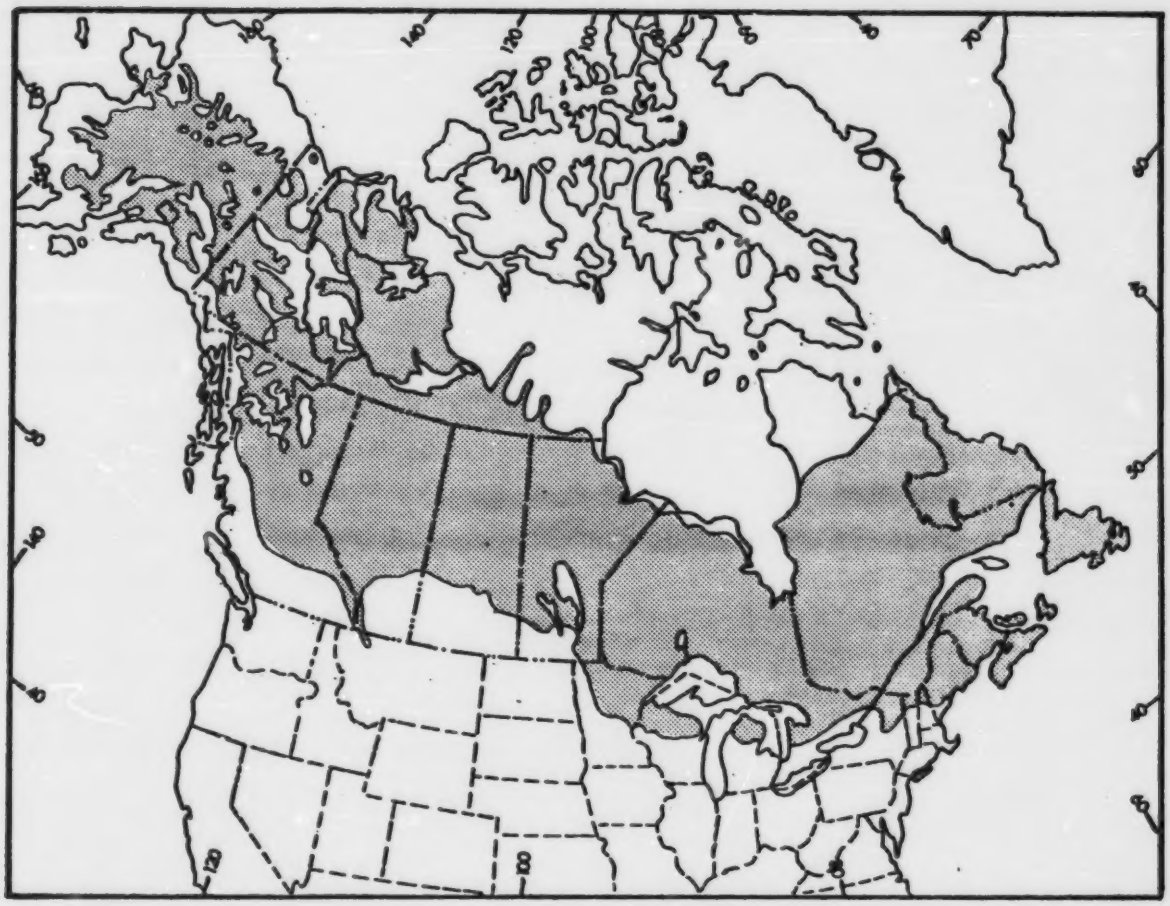

Figure 7. The range of white spruce (adapted from Fowells 1965; Hosie 1973).

The seeds are small (about 530 000/kg) and only those in the centre of the cones are viable (Fowells 1965). For trees in Minnesota, Roe (1952) reported 271 000 viable seeds, and a 75 year old tree in Canada yielded 184 000 seeds per tree (Tripp and Hedlin 1956). Waldron (1963) calculated that perhaps 3.7×10^6 viable seeds fall per hectare in central Manitoba on a moderate seed year, and over a 10 year period, approximately 16.6×10^6 viable seeds fall per hectare. Seeds are readily eaten by a variety of wildlife with those surviving usually germinating the following summer. Squirrels may consume most of the seed in light and moderate seed production years (Rowe 1955).

The young, first-year tree grows slowly and the root penetrates only several centimetres. The seedbed must remain moist, at or near the surface, or the seedling perishes (Place 1955). Light- to medium-textured, continually moist, exposed mineral soils are considered to be the best seedbed following disturbance (Rowe 1970), while under natural vegetation, decayed wood and stumps are considered to be the best (Fowells 1965). Major competition appears to come from the herbaceous understory which uses available light and draws on moisture at depths greater than the short seedling root can reach.

Many seedlings die after the first year due to shading and other competitive factors, suitability of the site, and damage by wildlife (the latter has been well-documented by a number of authors, as cited by Green 1978). Once established, growth depends on site fertility, moisture availability, and on the nature of the overstory. Baker (1949) rated white spruce as tolerant to competition. Lees (1966) noted a considerable increase in height and diameter when spruce were "released" following selective removal of aspen. Annual diameter increases were greatest when spruce were 20 to 40 years old; annual height increments were greatest when trees were 30 to 50 years old. White spruce still responds well to release after 40 to 50 years of suppression (Fowells 1965).

Various natural enemies attack white spruce in all stages of its life history. The seed is attacked by several minor insect pests and three major ones -- spruce seedworm, spruce cone maggot, and cone borers. In addition, numerous birds and small mammals, largely rodents, feed on the seed. Three major insect pests attack mature spruce, the spruce budworm (largely in stands where balsam fir is abundant), the European spruce sawfly (largely along the east coast), and the eastern spruce beetle (throughout the range). White spruce is said to be devoid of serious fungal injuries (Fowells 1965; Sutton 1969).

White spruce is much less sensitive to SO_2 than balsam poplar, jack pine, tamarack, white birch, and trembling aspen. Visible foliar injury results from exposure to SO_2 levels of 0.5 ppm for 8 h, 0.6 ppm for about 5.5 h, 0.7 ppm for about 3.5 h, 0.8 ppm for 2 h, and about 0.85 ppm for 1 h (Dreisinger and McGovern 1970, cited by Loman 1975). White spruce was the only conifer (along with the deciduous paper birch) to still be alive, although apparently dying, as close as 17 km downwind of an iron sintering plant emitting 90 000 t of "sulphur" for 11 years near Wawa, Ontario. White spruce seedlings, however, were not present within 25 km of the plant (Gordon and Gorham 1963). Winner and Bewley (1978) also reported that white spruce seedling numbers were lower than normal in heavily SO_2 stressed sites near petroleum refineries in the Alberta Rocky Mountain foothills, indicating that SO_2 stress decreases the reproductive success of white spruce. This may have been the result of reduced growth rates and cone production, inability of moist pollen to germinate, or changes in canopy cover making the seedlings more susceptible to frost.

Spruce needles injured by SO_2 experienced a higher incidence of foliar fungus infection instead of a decrease as occurred with other species such as aspen (Treshow 1975). Mycorrhizal associations in spruce injured by SO_2 have also been reported to be abnormal; the Hartig net was sometimes hypertrophic and the mantle thinner, tuft-like, or even absent (Threshow 1975).

Two western varieties of white spruce have been named (Sutton 1969; Hosie 1973). Natural hybridization is common with Engelmann spruce (*Picea engelmannii*) (e.g., see La Roi and Dugle 1968; Habeck and Weaver 1969; Daubenmire 1974) and Sitka spruce (*P. sitchensis*) but it is rare with black spruce (*P. mariana*) (Nienstaedt and Teich 1971).

White spruce is one of the most important trees in Canada for pulpwood and lumber (Hosie 1973). Yield estimates for white spruce stands vary with site conditions. Yields of 370 m^3/ha have been reported for 150 year old mixed spruce-poplar stands in the Lower Peace River (Lacate et al. 1965). These values are similar to Johnstone's (1977) data for the Mixedwood Section of Alberta. In the Mixedwood Section of Saskatchewan, similar values are reported but the best sites exceed 455 m^3/ha at maturity (Kabzems et al. 1976). Peterson and Levinsohn (1977), however, only reported total volumes of 243 m^3/ha for white spruce-aspen stands on the west half of Syncruce Lease 17, southwest of Fort MacKay. Estimated volumes for 200 year old stands in interior Alaska are about 310 m^3/ha (Fowells 1965).

On the AOSERP study area, Stringer (1976) sampled only one site which he considered as white spruce dominated. He considered most of the other stands in the same cluster (his "Upland White Spruce-Aspen Forest") as successional since balsam poplar was the secondary species in many stands where white spruce was dominant. Perhaps the name "Upland White Spruce-Poplar" would be more descriptive. Peterson and Levinsohn (1977) described a floristically similar type (their white spruce-aspen) covering about 18% of the west half of Syncrude Lease 17, southwest of Fort MacKay.

Stringer (1976) considered the understory to be quite distinct with *Alnus crispa* being relatively important in several stands. These successional stands are initially dominated by aspen, *Rosa acicularis, Viburnum edule, Vaccinium myrtilloides, Petasites palmatus*, and *Rubus pubescens* while *Ribes triste, Ledum*

groenlandicum, Aralia nudicaulis, Cornus canadensis, Linnaea borealis, and *Vaccinium vitis-idaea* are important and seem to persist as white spruce becomes dominant.

Other common but less important understory species included: the grasses *Calamagrostis canadensis, Schizachne purpurascens*, and *Elymus innovatus*; the forbs *Aster cillolatus, Epilobium angustifolium, Fragaria virginiana, Galium triflorum, Lathyrus ochroleucus, Maianthemum canadense, Mertensia paniculata, Mitella nuda, Pyrola asarifolia, P. secunda, Vaccinium vitisidaea*, and *Viola renifolia*; and the horsetail *Equisetum sylvaticum*. He noted a number of what could be considered successional stages of mosses, lichens, and liverworts on various organic substrates as decomposition and overstory changes occur. In stands still overtopped by aspen and other hardwoods, bryophytes and lichens occurred only on logs, stumps, and tree bases not covered by leaf fall. Only when the overstory was primarily closed-canopy conifers (no deciduous leaf fall) was the forest floor covered by mosses and lichens. The feather-mosses *Pleurozium schreberi* and *Hylocomium splendens* were most abundant, with scatterings of the mosses *Ptilium crista-castrensis* and *Rhytidiadelphus triquetrus* and the lichens *Cladina arbuscula, Peltigera aphthosa, P. canina*, and *P. polydactyla*.

When the vascular plants of the above list are compared to the canopy specificity rating developed by Dix and Swan (1971), there is fairly good agreement. Most of those listed showed a high or moderate "preference" for aspen dominated stands at Candle Lake, Saskatchewan, the exceptions being *Mertensia paniculata* and *Mitella nuda* (which appeared to "prefer" spruce overstory). Overall, this tends to support Stringer's contention that most of the stands he sampled are successional in nature.

On stands heavily dominated by white spruce in Wood Buffalo National Park, Raup (1935) listed as "primary" species *Picea glauca* and *Salix bebbiana* and the mosses *Ptilium crista-castrensis* and *Pleurozium schreberi*. He described the "secondary" species as "much scattered in their distribution" and noted that

one could walk for hundreds of metres where mosses comprised the only understory. These stands were dominated by a closed spruce canopy and contained a 10 to 15 cm layer of organic litter on the soil surface. Raup (1946) found three types of the spruce forest on the Athabasca-Great Slave Lake region which extends from the northern tip of the AOSERP study area: (1) the Park Like White Spruce Forest; (2) the Flood Plain White Spruce Forest; and (3) the Upland Mesophytic White Spruce Forest.

The first type is represented on the south shore area of Lake Athabasca in the AOSERP study area (Raup 1946) and in the Mixedwood Section of Saskatchewan (Kabzems et al. 1976). The understory species appear similar to those of jack pine on sandy sites and black spruce on stony sites.

Stringer (1976) does not report the second type, although some of his sites will likely approach it through time. Raup (1946) found this type on the higher portions of deltas and river floodplains, often in narrow strips separated by wet-to-semiaquatic types due to the continual erosion-deposition cycles often found there. "Primary" species were *Picea glauca, Salix bebbiana, Viburnum edule*, and *Cornus stolonifera*. Approximately half the species listed in these aspen stands being invaded by white spruce previously discussed (Stringer 1976) were also listed by Raup (1946).

The third type, the Upland Mesophytic White Spruce Forest, was found on rolling uplands along the lower Athabasca and lower Peace Rivers and to the west of the Slave River. It occurred mainly where drainage was sufficient to prevent the formation of muskeg, often on the lighter textured soils, particularly on lower slopes and hollows. "Primary" species (Raup 1946) included *Picea glauca* and *Salix bebbiana* and the mosses *Ptilium crista-castrensis* and *Pleurozium schreberi*. The understory included *Equisetum sylvaticum* and *E. scirpoides*, again with approximately half the species listed matching those discussed by Stringer (1976).

Raup (1946) observed white spruce stands in the general area from Fort McMurray northward about 80 km. The "primary" species listed were *Picea glauca* and *Populus tremuloides* with about 65 "secondary" species. Although he acknowledged the difficulty of defining the main understory species, he listed *Shepherdia canadensis, Prunus virginiana, Viburnum edule, Corylus cornuta*, and *Rosa acicularis*. When compared with Stringer's (1976) cover-abundance classes for his Upland White Spruce and Aspen Forest, only *Viburnum edule* and *Rosa acicularis* appeared to have similar status. *Shepherdia canadensis* appeared only occasionally and *Corylus cornuta* and *Prunus virginiana* are not even included in Stringer's species list. The two authors listed many species in common, but their relative importances were somewhat different. It appears that white spruce stands have highly variable understories with a few consistent species strongly related to both the composition and density of the overstory and to the substrate.

3.1.6 Black Spruce (*Picea mariana*)

Black spruce is the other major characteristic species of the boreal forest (Rowe 1972). It spans North America from the Atlantic Ocean (Maritimes and New England) to the Bering Sea (Figure 8). Usually a slow-growing tree averaging 9 to 15 m in height and 15 to 25 cm in diameter, it may reach heights of 30 m and diameters of 90 cm under favourable conditions but it is also reduced to a shrub in tundra areas near treeline.

As with white spruce, it is the major self-perpetuating dominant in the absence of disturbance. Depending on site conditions, white or black spruce may be dominant (Lewis et al. 1928). Moss (1955) concluded that, in Alberta, black spruce eventually dominates because black spruce can tolerate wetter and more nutrient poor sites. As peat accumulates, a site's nutrient status often decreases, which partially explains the common stunted aspect of trees in central areas of muskeg and the robust growth along margins. Although most people immediately associate

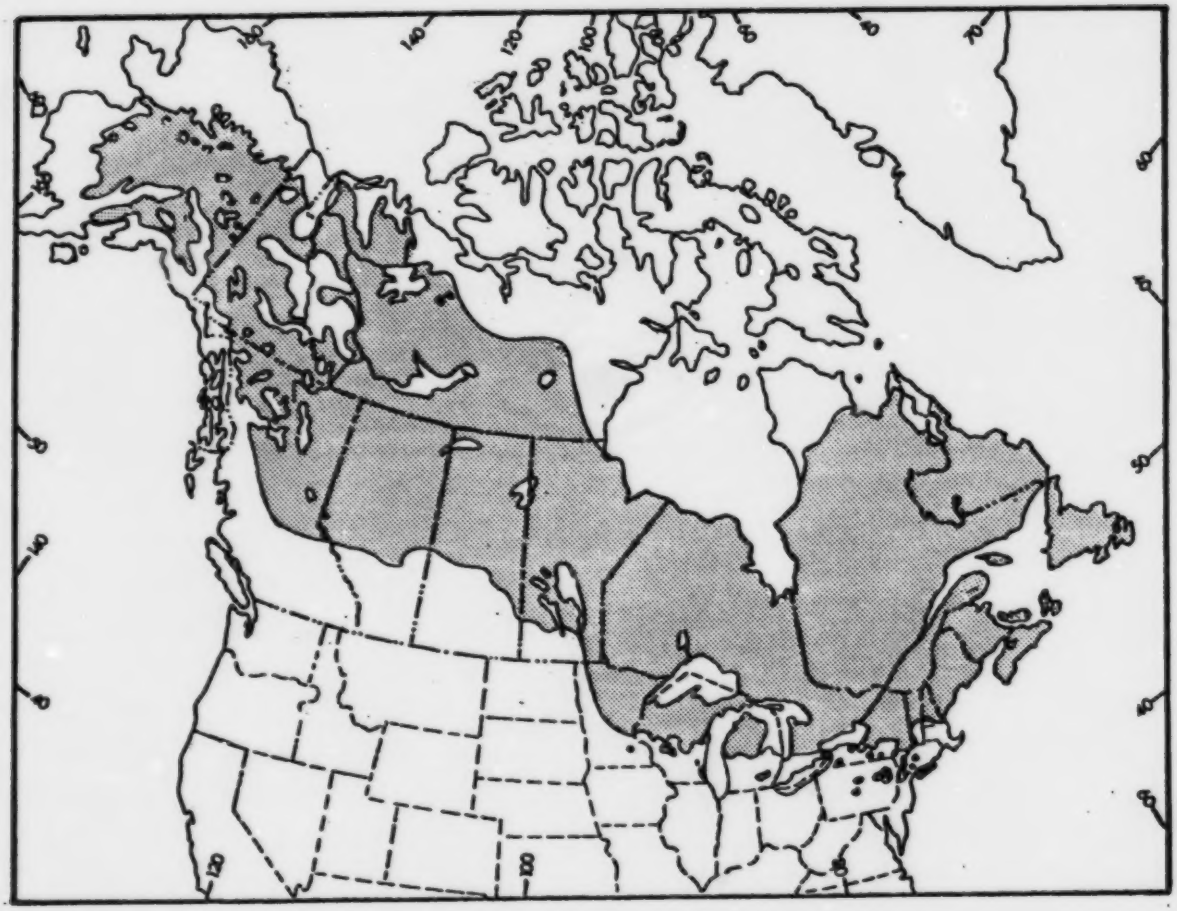

Figure 8. The range of black spruce (adapted from Fowells 1965; Hosie 1973).

black spruce with these wet conditions in western Canada, it is found on a variety of sites, some of which are considered relatively xeric. On wet sites, black spruce develops a wide-spreading mass of many rootlets just below the surface, but on well-drained sites, roots can penetrate deeper. Black spruce can tolerate relatively low nutrient levels (Sjors 1961; Jeglum et al. 1971) although it grows better where nutrients are higher. These two factors, roots which can adapt to various water table depths and tolerance of low nutrient, may well explain why it is competitive on such a variety of sites. It can compete with jack pine on sands and yet is also characteristic of muskeg areas and can occupy most habitats in between.

Dix and Swan (1971) classified black spruce as a "Chiefly pioneer" species. It produces cones every year and heavy crops about every 4 years (Fowells 1965). The cones are persistent and semi-serotinous, most seeds being shed within the first few years on a year-round basis (LeBarron 1948). The very small seeds (900 000/kg) may survive for many years in the cones. They remain viable and uninjured by fire which causes ones to open, releasing seed for recolonization. Apparently, wind dispersal of the winged seeds is limited. LeBarron (1948) found only 30% as much seedfall in the center of a 30 m clearcut strip as compared to that within the stand. In black spruce stands, seedfall may be 1.2×10^6 seed/ha but 0.5×10^6 is more common (Fowells 1965). Rodents such as red squirrels utilize seed and cones, greatly reducing seed availability (Fowells 1965).

Over 1 year on a New Brunswick upland, germination was 66% on mineral soil, 72% on burned duff, 47% on scarified duff, and 53% on weedy plots (Place 1955). LeBarron (1944) found germination was 46%, 29%, and 7% on mineral soil, burned duff, and undisturbed duff, respectively, in Minnesota. In central Newfoundland, Van Nostrand (1971) found germination on sphagnum moss three times lower than on mineral soil and lower yet on feather moss.

He further stated that even though sphagnum is a good germination medium, it is deficient in the nutrients necessary to produce healthy seedlings. Roe (1949) found that sphagnum sometime outgrew the black spruce seedlings and smothered them.

As was true for white spruce, moisture appears to play an important role in the establishment of black spruce seedlings. During wet years, upland sites often have enough moisture for establishment while during dry years they do not. A seedbed of feather moss may be more favorable than sphagnum during wet years (Place 1955).

The root system of black spruce seedlings is even less extensive than that of white spruce. The first year's root growth is reported to be about 5 cm in mineral soil and less than 4 cm in 2 years in sphagnum and feather moss (Fowells 1965). This is not conductive to survival during dry years or even during normal years on many sites. Once the seedlings reach several years of age, the root system becomes somewhat more extensive (usually more laterally than vertically) and mortality from drought decreases. Growth rates are determined by nutrient and moisture status and competition for light.

Vegetative reproduction can occur in black spruce by "layering", a process in which branches buried in the organic soil or moss take root. In addition, vegetative shoots can develop from adventitious buds on near-surface roots (Horton and Lees 1961).

Black spruce is considered to be tolerant to competition. Logan (1969) found that black spruce reared for 9 years at 13%, 25%, 45%, and 100% of full sunlight responded by increases in height and weight of shoots and root as light intensity increased. Baker (1949) considered black spruce to be slightly less tolerant to shade than white spruce, but Logan (1969) found black spruce to be taller and heavier than white spruce at all but the lowest light intensities.

Black spruce is relatively free of serious fungal defects other than butt rots, and it has a reputation for relative

freedom from insect losses. Butt rots are common in upland stands at about 100 years of age. Black spruce dwarf mistletoes, though common in the east, are virtually absent west of Manitoba. Spruce budworm occasionally defoliates spruce, but spruce is not a preferred food (Vincent 1965).

Black spruce may be more sensitive to SO_2 than white spruce. It was not present as close to the iron sintering plant emitting 90 000 t of sulphur per year for 11 years at Wawa, Ontario, as white spruce. Living but reddened or chlorotic trees were not present within 25 km of the plant. No black spruce seedlings were closer than 25 km from the plant (Gordon and Gorham 1963).

Spruce needles injured by SO_2 experienced a higher incidence of foliar fungal infection instead of the decrease reported for other species such as aspen (Treshow 1975). Mycorrhizal associations in spruce injured by SO_2 have also been reported to be abnormal (Treshow 1975).

Photoperiodic ecotypes of black spruce have been demonstrated and races are likely to exist. Natural hybrids have been reported with red spruce (*Picea rubens*) but introgressive hybridization is infrequent and gene flow is limited (Gordon 1976).

The principal use of black spruce is as pulpwood. The long fibres in black spruce add strength, making it a favored species for the manufacture of facial tissues and other paper products. It is not used for raw timber to the same extent as other spruce (Hosie 1973). Volumes of black spruce have been measured at about 190 to 210 m^3/ha at a rotation age of 90 years and 210 to 230 m^3/ha at maturity (110 to 120 year old stands) on the best sites of the Mixedwood Section of Saskatchewan (Kabzems et al. 1976), but Peterson and Levisohn (1977) only reported gross yields of 94 m^3/ha for black spruce-feathermoss stands in the west half of Syncrude Lease 17 southwest of Fort McKay.

Stringer (1976) found black spruce dominated stands to be common in the AOSERP study area. He identified a "Black Spruce Bog Forest" and an "Upland Mixedwood and Coniferous Forest".

In the Black Spruce Bog Forest, the ground cover was low in stature with the tall species being mainly the low shrubs *Ledum groenlandicum* and the considerably less abundant *Vaccinium Myrtilloides*. Also present but missing from some sites were scattered plants or small patches of *Betula glandulosa, Salix glauca, S. myrtillifolia*, and *Chamaedaphne calyculata*. Below the shrub layer the most prominent species were *Equisetum sylvaticum, Oxycoccus microcarpus, Rubus chamaemorus*, and *Vaccinium vitis-idaea* and lesser amounts of *Smilacina trifolia* and *Eriophorum vaginatum*.

In the Upland Mixedwoods and Coniferous Forest, black spruce was also dominant (Stringer 1976). The understory was again low in stature with scattered tall shrubs, *Salix bebbiana* and *Alnus crispa*. *Ledum groenlandicum* and *Vaccinium myrtilloides* were abundant in the shrub stratum. The low shrub-herb stratum constantly and prominently contained *Vaccinium vitis-idaea*. Herbaceous cover was variable, with the herb *Cornus canadensis* and the grass *Elymus innovatus* seemingly being the most consistent and important species. The ground surface was described as being almost completely covered by bryophytes and lichens, the most common mosses being *Pleurozium schreberi, Hylocomium splendens*, and *Dicranum polysetum* and less abundantly *Polytrichum juniperinum*. The most common lichens were *Cladina mitis* and *C. alpestris* and less abundantly *Peltigera malacea, Cetraria nivalis, Cladina rangiferina*, and *C. arbuscula*.

On upland black spruce stands at Candle Lake, Saskatchewan, only *Vaccinium vitis-idaea* was included in the high specificity group for canopy types dominated by black spruce. (Non-vascular plants were not rated.) However, *V. vitis-idaea* occurred much more consistently under jack pine canopies. In fact, most of the species listed as understory of black spruce stands showed only intermediate or low specificity for canopy types. Lichen cover was second to moss cover and only rose above 6% in jack pine and black spruce stands. Common lichens were *Cladonia gracilis, C. mitis, C. rangiferina*, and *C. alpestris*; common mosses were *Pleurozium schreberi Hylocomium splendens*, and *Ptilium crista-castrensis*.

The early work of Lewis and Dowding (1926) in the Edmonton area of Alberta described the muskegs as typified by the primary species of *Ledum groenlandicum*, *Sphagnum capillaceum*, *Vaccinium vitis-idaea*, and *Rubus chamaemorus*. Most of the muskeg was dominated by *Picea mariana* with *Betula* spp. and *Larix laricina* also present. Mosses and lichens were similar to those listed by Stringer (1976) above. They described the areas as dynamic and used the term "retrogressing" because fire and in-flow of water was changing nutrient status and pH.

A peat-filled basin in sand hill terrain 90 km north of Edmonton contained two types of black spruce stands (Lewis et al. 1928). On shallower sphagnum peat, the major understory species were *Ledum groenlandicum*, with frequent occurrence of *Sphagnum capillaceum* and *Vaccinium vitis-idaea* and, rarely, *Oxycoccus* spp. On deeper sphagnum peat and closer to the sandy slopes (with some sand having drifted into the peat), the understory vegetation was dominated by *Vaccinum myrtilloides* and *Ledum groenlandicum*, with occasional plants of *Polytrichum juniperinum*, *P. commune*, and *Equisetum sylvaticum* and, rarely, *Vaccinium vitis-idaea*. This understory was thus much more site-specific than the overstory trees. Mature muskeg was described as being dominated by close growing, old black spruce trees with small trees and seedlings of white spruce. The understory was dominated by *Ledum groenlandicum* with rare patches of live *Sphagnum* spp. on mostly dead sphagnum mounds. *Vaccinium vitis-idaea* was quite common and appeared to be covering the peat mounds. *Ribes* spp. were also abundant, *Equisetum sylvaticum*, common, and *Cladonia pyxidata*, present. Similar types have been described for the Mixedwood Section of Saskatchewan (Kabzems et al. 1976).

In Wood Buffalo National Park and the Lake Athabasca-Great Slave Lake region, the understory in black spruce dominated bog forests varied greatly (Raup 1935, 1946, respectively). Dominant understory species were *Ledum groenlandicum* with *Sphagnum* spp. in wetter conditions and *Ptilium crista-castrensis* and *Pleurozium schreberi* in dryer conditions. *Larix laricina* was usually present as trees and seedlings in varying amounts.

"Secondary" species are too numerous to list; however, they were the same ones that were discussed by Stringer (1976) for the AOSERP study area. This included a number found in white spruce stands and others, such as *Carex* spp., more characteristic of wetlands. Raup (1946) found it difficult to select a list of secondary species due to the interaction of succession, a changing water regime, and landforms. This interaction creates a wide variety of micro-habitats where remnants of earlier succession stages can survive and "pioneers" from future stages can mix with those in the current stage dominant.

Moss (1953b, 1955) stated that there are two main black spruce associations in Alberta--the Black Spruce-Feather Moss Association and the Black Spruce Bog-Moss Association. As the name implies, the first association was dominated by *Picea mariana* and *Hylocomium splendens*. It frequently contained *Picea glauca, Populus tremuloides*, and *Salix* spp. Other important species included *Ledum groenlandicum, Vaccinium vitis-idaea, Rosa* spp., *Ribes* spp., *Equisetum* spp., *Cornus canadensis, Petasites palmatus, Linnaea borealis, Mitella nuda, Rubus pubescens*, and *Carex* spp. and the lichens *Peltigera aphthosa* and *Cladonia* spp. The second type, the Black Spruce Bog-moss Association, was characterized by *Picea mariana* trees frequently with *Larix laricina, Betula papyrifera* and *Salix* spp. The forest floor was covered with bog mosses (*Sphagnum* spp.) and by several species of lichens (*Cladonia* spp.). The major vascular plants listed were *Ledum groenlandicum, Vaccinium vitis-idaea, Rubus chamaemorus*, and *Smilacina trifolia*. Similar types with many of the same dominants are typical of imperfectly to very poorly drained sites in the Mixedwood Section of Saskatchewan (Kabzems et al. 1976).

Although these black spruce dominated stands are often quite wet, they occur wherever a depressional situation allows them to develop. On the AOSERP study area, for example, Stringer (1976) found black spruce stands of the types described by Moss (1953a, 1953b, 1955) on the slopes of the Birch Mountains, Stony Mountain Uplands, and the gentler slopes of the Thickwood Hills, as well as in the relatively flat area between the Athabasca River and the Muskeg Mountains.

3.1.7 Tamarack (*Larix laricina*)

Tamarack or larch is commonly encountered in stands of scattered trees and less often in dense stands in bog-fen complexes. A deciduous conifer, it has one of the widest ranges of the North American conifers, a range very similar to white and black spruce (Figure 9). Tamarack is a small- to medium-sized tree about 9 to 21 m tall and 30 to 60 cm in diameter (Hosie 1973).

Tamarack is considered to be primarily a pioneer tree species in fens and bogs in Canada (Moss 1953a; Ritchie 1957, 1960). It is most commonly found growing in moist organic soils such as peats and mucks (Van Dersal 1938; Fowells 1965; Viereck and Little 1972). In Alaska, it grows in dense stands on flood plains (often with white and black spruce) as well as on well-drained uplands where its growth rate equals that of white spruce (Viereck and Little 1972). Van Dersal (1938) reported that it was quite intolerant of droughty sites in the border states of central and eastern United States. It is characteristic of swamps and bogs, and further north it also occupies drier sites, usually in a mixture with other species (Fowells 1965).

Tamarack apparently is a shallow rooter. Under wet conditions, roots can be found at the surface spreading several metres and sometimes fused with roots from adjacent trees (Lewis et al. 1928). Apparently, tamarack does not root deeply even on uplands. In northern Ontario on sandy soil, rooting was usually no more than 30 to 60 cm below the surface (Bannan 1940). Most authors agree that soil texture is not limiting for the species, as it reportedly grows on all textural classes.

At Candle Lake, Saskatchewan, Jeglum (1968) studied water-table depth, nutrient status, and pH at the 15 cm depth in the three stands where it attained its highest average quantitative value. They were: a treed stand with approximately 250 to 500 trees/ha, a sapling stand with almost 2500 saplings/ha, and a seedling stand with almost 5000 seedlings/ha. Tree and sapling stands occurred where the water table was at the

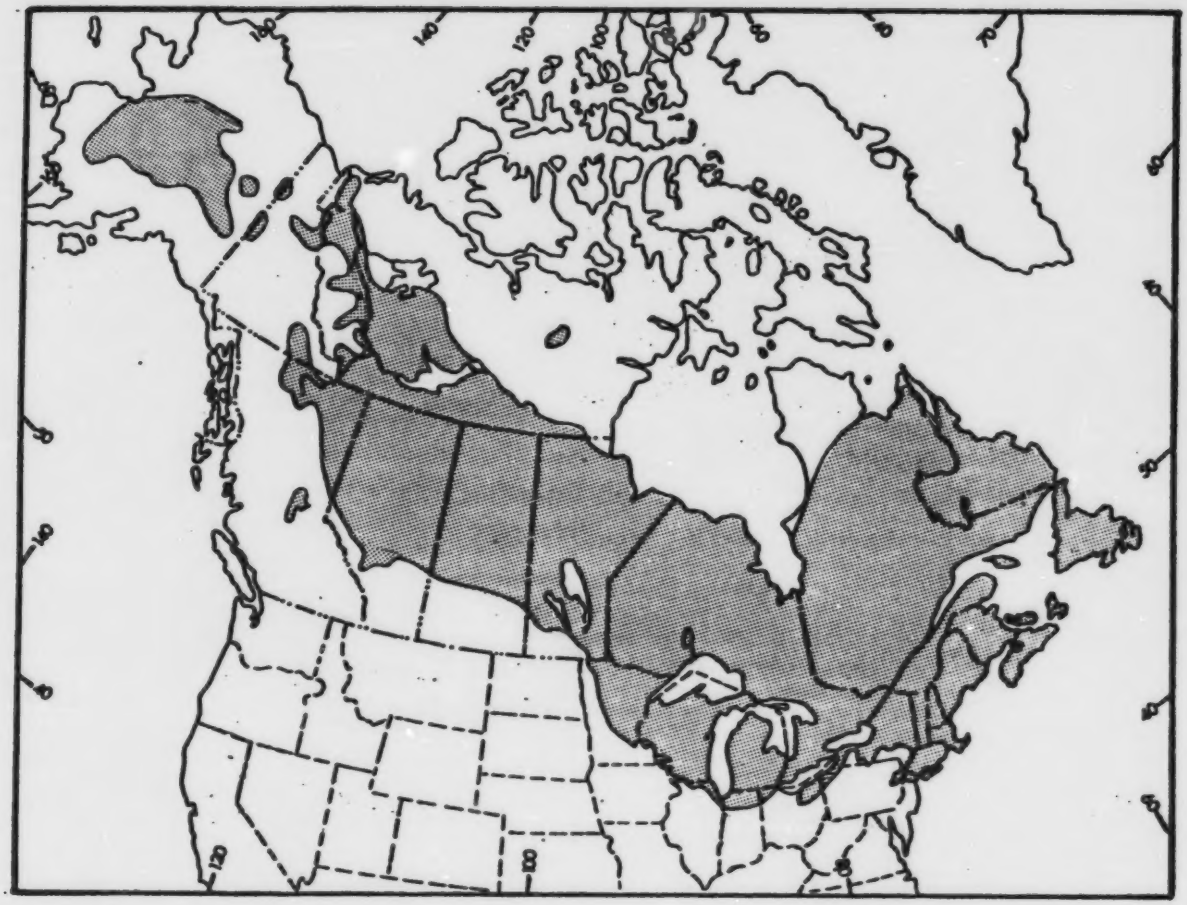

Figure 9. The range of tamarack (adapted from Fowells 1965; Hosie 1973; Viereck and Little 1972).

surface or, at most, 50 cm deep, whereas in the seedling stand it was 5 to 60 cm below the surface. Nutrient status in all three stands was found to indicate a tolerance, if not a preference, for relatively low nutrient levels. Seedlings grew on soils of pH 3.5 to 6.5, saplings from pH 6.0 to 6.5, and trees from pH 6.5 to approximately 7.5. A later paper from the same data for all stands sampled reported tamarack stands on sites ranging from pH 3 to almost pH 8 (Jeglum 1971).

Seed production in Minnesota was best in open, vigorous stands with trees between 50 and 150 years old (Duncan 1954). The seeds were small, ranging from 460 000 to 930 000/kg, but Van Dersal (1938) reported only 200 000/kg. An open, 80 year old stand produced 3.75×10^6 to 6.25×10^6 seeds/ha, with a closed stand producing considerably less (1.25×10^6 to 3.0×10^6/ha). During an exceptional year, as many as 12.5×10^6/ha might be produced (Duncan 1954). Few seeds are scattered farther from the parent tree than twice its height. Seeds fall the season they ripen, although the empty cones may stay on the tree for several seasons. Up to 50% of the seeds produced may be lost to rodents; with other losses, only 5 to 10% may finally germinate.

The best seedbed in Alberta is apparently moist mineral or organic soil with a light covering of forbs and/or grasses but with no appreciable amount of shrubs (Beeftink 1951). Moist mosses, including slow growing *Sphagnum* spp., may be an excellent seedbed if flooding does not occur. If it does, fast growing *Sphagnum* may smother the small delicate seedling (Duncan 1954).

Tamarack seedlings are very small the first 2 months after germination; losses are high from damping off, drought, drowing, or insect pests. First-year growth on sites with high densities may only be 2.5 cm while on ideal sites at low densities, growth of 10 to 13 cm can occur (Duncan 1954). In Alberta, on wet, cold muskeg, only 1 to 5 cm of growth occurs annually for up to 8 years (Beeftink 1951). On well-drained but moist sites in Minnesota, tamarack is one of the fastest growing conifers (Conway

1949) and on favorable sites in Alberta an annual height increment of 45 cm may occur the first 20 to 25 years (Beeftink 1951).

Tamarack is very intolerant to shade and must be in the dominant stratum to survive (Baker 1949; Duncan 1954). Although young seedlings appear to be slightly tolerant to shade, losses occur due to shading causing natural thinning. As a result, tamarack maintains itself only in relatively open stands.

Various insect pests attack tamarack. The most important is the larch sawfly (Kabzems et al. 1976) which periodically becomes epidemic and defoliates large areas for several successive years; growth is greatly reduced and many trees die. Insect pests also attack developing seeds and seedlings. Fungal pests cause early losses of seedlings by damping-off diseases. In trees, fungi cause heart rot, butt rot, root rot, and various needle diseases or rusts. Tamarack seedlings are eaten by snowshoe hare in Alberta (Beeftink 1951) and by porcupines and deer elsewhere (Fowells 1965).

In sensitivity to SO_2, tamarack is roughly similar to jack pine and white birch (Dreisinger and McGovern 1970, cited by Loman et al. 1972). Downwind of the iron sintering plant emitting 90 000 t of "sulphur" annually for 11 years at Wawa, Ontario, tamarack was only present more than 25 km from the plant but the trees exhibited foliar injury. Beyond 32 km, signs of damage for canopy species were not obvious. Tamarack seedlings were not present in the study area in sufficient numbers even in the unaffected area to be listed by Gordon and Gorham (1963).

No specific races of tamarack have been generally accepted. A hybrid between tamarack as the female parent and European larch (*Larix decidua*) has been produced in Denmark (Johnson 1939).

Tamarack is a heavy, strong softwood, resistant to decay. It is used for railway ties, poles, posts, pilings, boxes, and crates. It may also be used for boat-building and pulpwood (Kabzems et al. 1976; Hosie 1973). Maximum production of tamarack in stands in the Mixedwood Section of Saskatchewan is about

75 to 85 m^3/ha at about 100 to 130 years of age; total production in stands with equal amounts of tamarack and black spruce is about 140 m^3 (Kabzems et al. 1976).

Few of the stands sampled on the AOSERP study area (Stringer 1976) contained tamarack. Of the 84 stands sampled, it was the single dominant on only two: one (of three) of the "Lightly-Forested Tamarack and Open Muskeg" and one (of eight) of the "Upland Mixedwood and Deciduous Forest". It was co-dominant in only one of the seven stands of the "Semi-Open Black Spruce Tamarack Bog Forest" and secondary in another. Of 12 stands in the "Black Spruce Bog Forest", it was secondary in only two. The understory species have been discussed previously (see "black spruce" and "white spruce" above) and will not be repeated here.

Detailed studies of wetlands in central Saskatchewan led Jeglum (1968, 1971, 1972, 1973) to classify tamarack stands into two types: a *Larix laricina* broad-leaf sedge type on more nutrient rich sites and a *Larix laricina* narrow-leaf sedge type on poorer sites. In the former, he listed tamarack as occurring as saplings (1250/ha) with *Ledum groenlandicum* providing more than 30% of the cover and *Equisetum fluviatile* over 90% cover. The mosses *Calliergon giganteum* and *Hypnum lindbergii* attained greater than 40% frequency-dominance (a measure of frequency in which a species was recorded as present in the quadrat only when it had a cover value of at least 25%). Tamarack of the *Larix laricina* narrow-leaf-sedge type also existed as saplings and seedlings (2500/ha). Also present were black spruce seedlings and the shrubs *Andromeda polifolia* and *Betula glandulifera* (over 20% cover). In the herb layer, species with greater than 80% frequency were *Calamagrostis inexpansa, Carex aquatilis, C. chordorrhiza, C. diandra-prairea, C. lasiocarpa, Menyanthes trifoliata*, and *Potentilla palustris* and the mosses *Aulacomnium palustris* and *Drepanocladus revolvens*. Similar types have been described for the Mixedwood Section of Saskatchewan (Kabzems et al. 1976).

Lewis et al. (1928) described a Larch-Birch-Drepanocladus moor 90 km north of Edmonton, Alberta. *Larix laricina* was the dominant tree, *Betula glandulosa* the dominant tall shrub, and *Drepanocladus revolvens* dominated the ground cover. *Tofieldia glutinosa* and *Equisetum fluviatile* were abundant and *Menyanthes trifoliata, Salix* spp., *Spiranthes* spp., *Eriophorum vaginatum*, and *Muhlenbergia racemosa* occurred frequently. In Wood Buffalo Park, *Picea mariana* and *Ledum groenlandicum* were the primary species to invade bogs, and although tamarack was quite common, it did not take a primary position (Raup 1935).

Moss (1953b) stated that floristically, tamarack stands are similar to the black spruce-peat moss association. Tamarack often becomes established on a *Drepanocladus-Carex-Betula* bog which is often invaded by *Sphagnum*, thereby eventually favoring black spruce invasion. In a study of several tamarack stands, considerable variability was noted due to "the complexity of factors affecting its development and perpetuation". Jeglum (1968) encountered more species in tamarack stands at Candle Lake, Saskatchewan, than in other types. Moss (1953b) listed 25 species of woody plants (eight *Salix*), 37 herbs (14 species of *Carex*), and 18 bryophytes (eight *Sphagnum*). Of the woody plants, *Larix laricina* was dominant; *Betula glandulosa* frequently locally abundant; *Picea mariana, Salix pedicellaris*, and *Ledum groenlandicum* occasionally locally abundant; and *Oxycoccus microcarpus* scattered but locally abundant. Of the herbs, only *Galium labradoricum, G. triflorum*, and *Rubus acaulis* were noted as occasionally locally abundant. In addition, although only seven species were rated as occasionally present and the remainder rare; together they provide a considerable amount of sedge cover. Bryophytes were quite important on the ground surface with *Aulacomnium palustre* and *Camptothecium nitens* noted as frequently locally abundant and *Drepanocladus* spp., *Hylocomium splendens, Sphagnum recurvum, S. magellanicum, S. capillaceum*, and *S. fuscum* as occasionally locally abundant. Moss (1955) subsequently included the herbs *Caltha palustris, Calamagrostis* spp., *Equisetum fluviatile*, and *Potentilla palustris* as being characteristic of the type.

3.1.8 Balsam Fir (*Abies balsamea*)

Balsam fir is the least abundant of the eight major tree species present on the AOSERP study area. Range maps in Halliday and Brown (1943), Fowells (1965), and Hosie (1973) show that the AOSERP study area is on the western and northern fringe of its range (Figure 10). In Canada, its highest density of occurrence is in the east.

In the Lake Athabasca area, balsam fir occurs on the more mesic sites in scattered stands in valleys and on north-facing slopes (Halliday and Brown 1943). Raup (1936, 1946) considered balsam fir a primary species only along the Clearwater and Athabasca rivers in the Fort McMurray area. It disappeared northward toward the Lake Athabasca Delta. It grew with white spruce and paper birch (his "Balsam Fir-White Spruce Forests"). Trees were 30 to 60 cm in diameter and approximately 30 m tall. These sites were normally wet and subject to flooding early in the season. Stringer (1976), however, found balsam fir only on upland sites in the AOSERP study area. Lacate et al. (1965) did not mention its presence on the lower Peace River in Wood Buffalo Park.

Moss (1953b) reported it mixed with white spruce, aspen, balsam poplar, and white birch on flat areas and gentle slopes south and southeast of Lesser Slave Lake. It occurred only locally in pure stands, the associated species being those commonly found with white spruce and the poplars.

In a study of spruce-fir forests of the highlands of northern Alberta, Achuff (1974) denoted four community types based on species dominance and abundance. Only four stands were close to the AOSERP study area. The closest two fell within the *Viburnum-Hylocomium* type. Only one of these stands contained more than a trace of balsam fir; it had approximately 20% fir crown cover. The other two stands fell within the *Calamagrostis canadensis* type. They had 22 and 16% fir crown cover.

Balsam fir is a small- to medium-sized tree, usually 15 to 21 m tall and 30 to 60 cm in diameter; somewhat larger trees

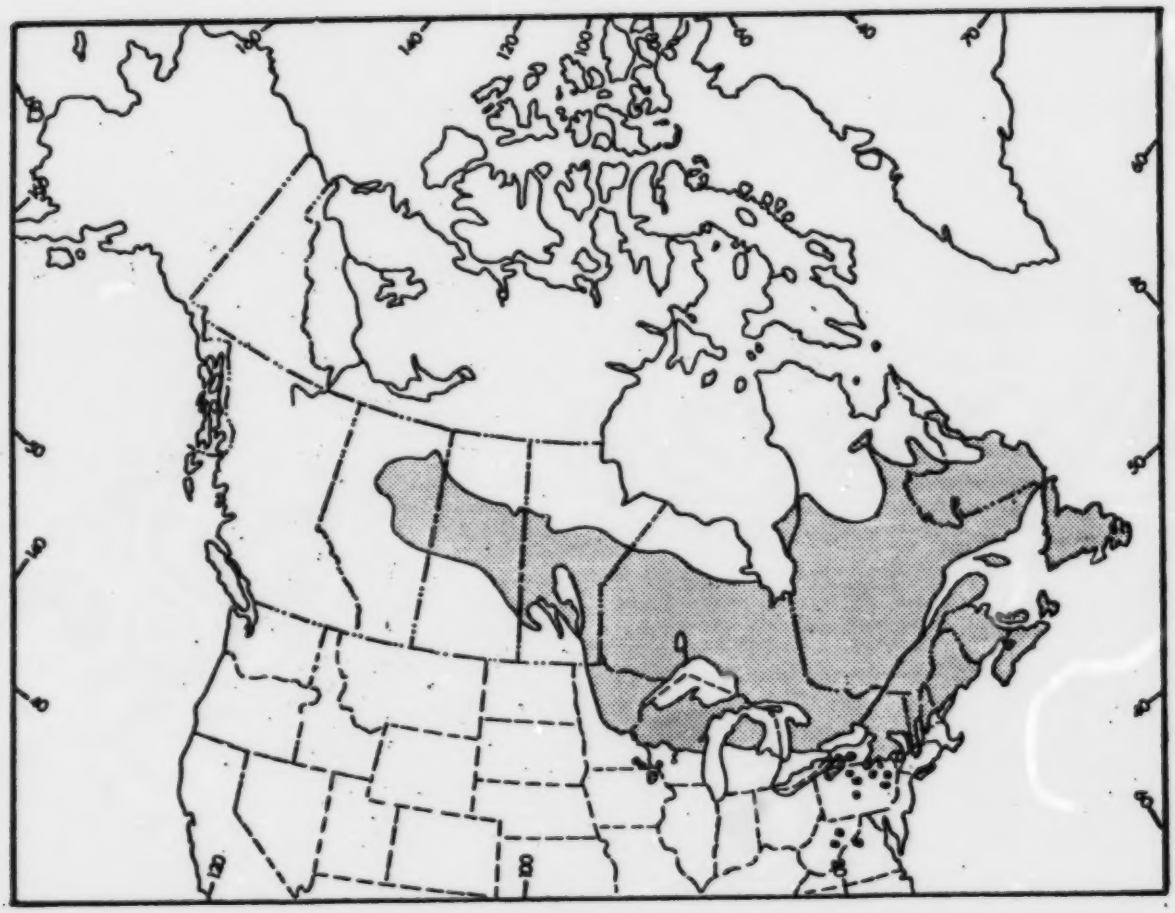

Figure 10. The range of balsam fir (adapted from Fowells 1965).

are occasionally found (Bakuzis and Hansen 1965). It is the only tree which Dix and Swan (1971) considered to be a late successional species.

Balsam fir will grow on a wide variety of soil textures, from gravely to silt loams and on peat soils (Bakuzis and Hansen 1965). At Candle Lake, Saskatchewan, it grew on dry to fairly wet sites and on soils ranging from sands to clay loams (Dix and Swan 1971). Most stands occurred on the lighter textured loams. Balsam fir will tolerate a wide range of pH values; however, more stands occurred at lower pH values with few in the pH 7 to pH 8 range.

Balsam fir apparently can be expected to produce exceptional seed crops every 2 to 4 years (Lutz 1956). The seeds are larger and heavier than the seeds of other conifers, averaging over 130 000/kg (Fowells 1965). Seeds are released toward the end of summer and most cones empty by the following spring. Seed is dispersed a maximum of about 150 m but it usually falls much closer due to the added weight of the adhering cone scales.

Germination is reported to be about 25% (Van Dersal 1938); however, it is related to the age of the parent tree (Benzie 1960). Maximum germination of 68% was reported for a 41 year old tree but it dropped to as low as 8% for seed from young or extremely old trees (160 years).

The main criterion for successful establishment of balsam fir seedlings is the presence of sufficient moisture to prevent drying of the germinated seed. The seedbed material makes little difference; the best germination and establishment takes place if the minimum light intensity is 15 to 20% of full sunlight (Place 1955). In a 9 year study of the effect of different light intensities (13, 25, 45, and 100% full light), Logan (1969) found best growth occurred under conditions of 45% full light. Somewhat less growth occurred under full light conditions followed closely by the 25% level. Fowells (1965) reported that balsam fir seedlings have long tap roots; this may account for the ability of the species to establish on various seed beds, including deep organic layers. In

view of its ability to reproduce and grow slowly under its own closed canopy, Dix and Swan's (1971) classification as a non-pioneer species appears fitting. When "released" through elimination of competition, young seedlings or saplings of balsam fir grow rapidly (Hosie 1973). Growth rates observed by Logan (1969) led him to believe that balsam fir would outgrow white spruce, itself a fairly rapid grower, at all light levels by the twelfth year.

Balsam fir has several insect and fungal enemies. The two most important insects are the spruce budworm and the balsam woolly aphid. One fungus can enter through stubs and broken tops, causing decay in living trees; the resulting losses are two to three times greater than those from butt rots. Butt rots, however, weaken trees sufficiently to make them most susceptible to wind damage. Rot may begin at 40 years of age and increases so that more than half of 70 year old trees are infected. In general, the drier the site, the greater the damage from rot (Fowells 1965).

Downwind of the iron sintering plant at Wawa, Ontario, emitting 90 000 t of "sulphur" annually for 11 years, balsam fir, though exhibiting foliar injury, were alive 25 km from the plant. Seedlings, however, grew as close as 19 km to the plant (Gordon and Gorham 1963).

No distinct geographic races of balsam fir are reported but two botanical varieties have been named (Fowells 1965). Two artificial crosses are reported with *A. lasiocarpa* and *A. fraseri* (Klaehn and Winieski 1962).

Balsam fir is a major pulpwood species. It is also sawn and marketed as "spruce" and used as a Christmas tree (Hosie 1973). Yields for fir and spruce-fir stands vary with site conditions. For 50 year old stands in eastern forests, total yield can range from 210 to 420 m^3/ha, but merchantable volumes approach only 70 to 90 m^3/ha.

On the AOSERP study area, balsam fir grows in mixed stands with both deciduous and coniferous species. The understory would probably be characterized by a decrease in species numbers with increases in canopy dominance by balsam fir, much as happens

when white spruce stands develop and mature. Dix and Swan's (1971) data (although hard to interpret for this purpose) indicated that at Candle Lake the most important species in balsam fir stands were also important in white spruce stands. There appeared to be considerably fewer species of vascular plants, however, under the balsam fir canopy. Moss cover was the highest in balsam fir stands making up 52% of the cover, whereas it provided 50 and 44% cover in black and white spruce stands, res-ectively.

Achuff (1974) sampled four spruce-fir stands near the southern boundary of the AOSERP study area. The closest two were in his *Viburnum-Hylocomium* type and the other two were in his *Calamagrostis canadensis* type. In the *Calamagrostis canadensis* type, balsam fir had about 20% mean cover, almost the same as white spruce, and was the only tree reproducing in the understory. Major shrubs were *Viburnum edule* and *Rubus strigosus* and, to a lesser extent, *Alnus crispa* and *Rosa acicularis*. Prominent species of the dwarf shrub-herb layer were *Calamagrostis canadensis, Cornus canadensis, Aralia nudicaulis, Rubus pubescens, Mitella nuda, Linnaea borealis, Equisetum sylvaticum,* and *Mertensia paniculata.* The bryoid layer was dominated by *Hylocomium splendens, Ptilium crista-castrensis,* and *Pleurozium schreberi.*

The two stands of the *Viburnum-Hylocomium* type closest to the AOSERP study area had about 30 to 40 white spruce cover and less than 8% balsam fir tree cover. Principal shrubs were *Viburnum edule* and *Rosa acicularis*. The principal species in the herb-dwarf shrub layer was *Linnaea borealis*; other abundant species included *Lycopodium annotinum, Cornus canadensis, Rubus pubescens, Mitella nuda, Mertensia paniculata, Pyrola asarifolia, Equisetum sylvaticum,* and *Aralia nudicaulis*. Mosses nearly covered the ground, with *Hylocomium splendens* contributing over half the total cover. Other important shrubs were *Pleurozium schreberi* and *Ptilium crista-castrensis.*

Stands clearly dominated by balsam fir were sampled on moister sites south of Lesser Slave Lake (Achuff 1974). Major species in the shrub layer were *Ledum groenlandicum* and balsam fir

seedlings and saplings. The herb-dwarf shrub layer was dominated by *Rubus pedatus*, *Cornus canadensis*, and *Vaccinium membranaceum*, with lesser amounts of *Linnaea borealis*, *Lycopodium annotinum*, *Vaccinium vitis-idaea*, and *Pyrola secunda*. The bryoid layer was dominated by *Pleurozium schreberi*, *Ptilium crista-castrensis*, and *Hylocomium splendens*.

The extent to which Achuff's (1974) data are applicable to the AOSERP study area is unknown. The *Viburnum-Hylocomium* type, however, is likely to occur in many upland spruce-dominated sites since it had a small balsam fir component and basically represents an upland mixedwood type.

3.2 IMPORTANT TALL SHRUBS

3.2.1 *Alnus tenuifolia* (River Alder)

Alnus tenuifolia has a widespread, largely boreal forest distribution (Figure 11), although it is somewhat indefinite, partly because of nomenclatural changes. (See, for example, Schopmeyer (1974); Scoggan (1978), in "Flora of Canada", called it *Alnus rugosa* var. *occidentalis*.) It is usually a slender shrub growing in dense thickets, but can sometimes become a small tree 6 to 7.5 m tall and up to 15 cm in diameter. Occasionally, trees on the best sites may reach 13.5 m in height and 25 cm in diameter (Hosie 1973).

Alnus tenuifolia is considered a species of wet but well-drained sites, mostly along the borders of streams and lakes and in gullies and swamps with some drainage (Moss 1959; Hosie 1973). It is rated as relatively intolerant of competition and, therefore, rarely grows with other trees (Hosie 1973). McGinnies (1972) also indicated it was a species of the margins or openings of the northern coniferous forest, and Wright (1972) reported it could recover quickly after a fire. Alders, as a group, have root nodules with symbiotic bacteria that are capable of fixing nitrogen, adding to soil fertility as the rootlets die and decay.

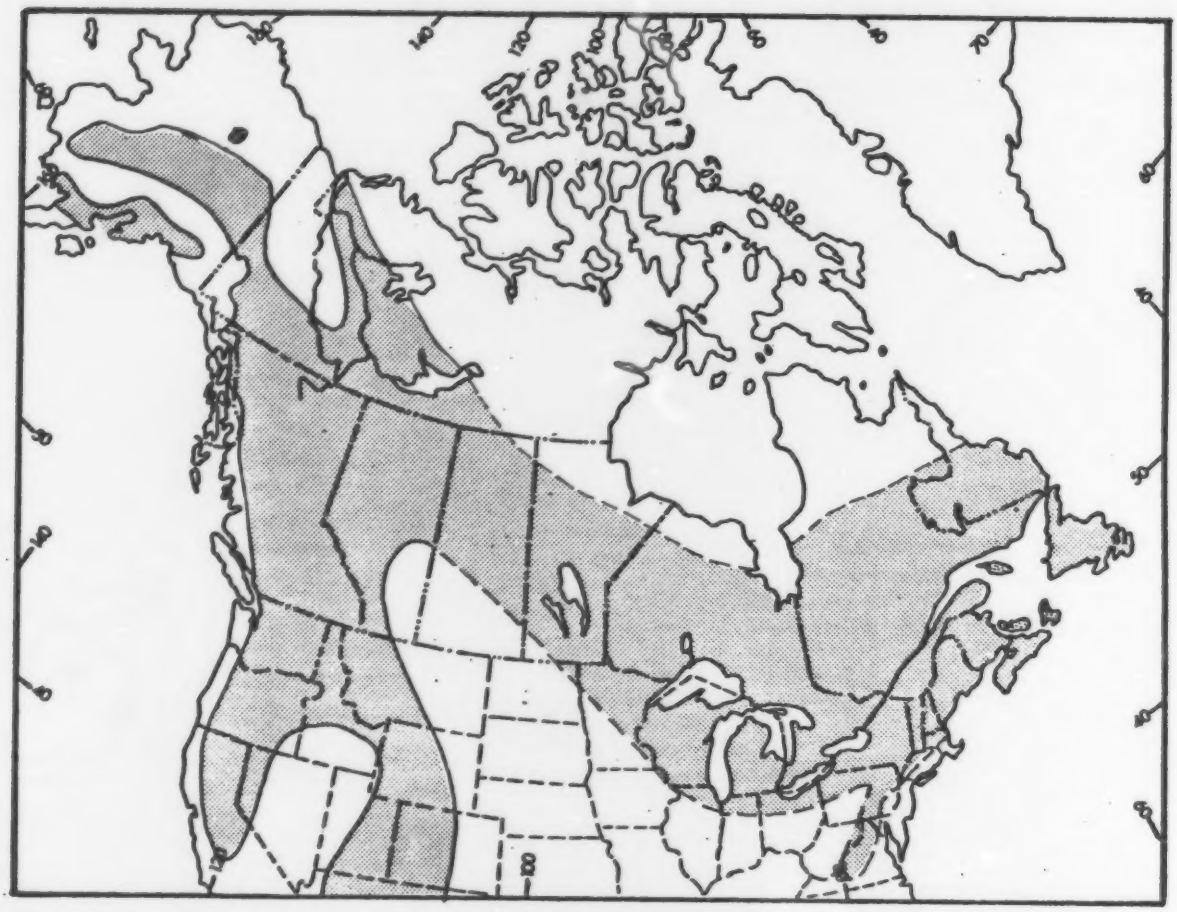

Figure 11. The range of *Alnus tenuifolia* (adapted from Hulten 1968; Viereck and Little 1972).

River alder flowers in early spring before the leaves unfold. Male and female flowers form separately but on the same twig. The mature fruit, which ripens by fall, is a small persistent cone 0.8 to 1.6 cm long. Seeds are small nuts, dispersed by wind or water. Seeds are light with 1 kg containing from 1.8 to 4.4×10^6 seeds. Less than 5% of these were full (Schopmeyer 1974). Germination of viable seeds is equally high with and without cold stratification.

Alnus tenuifolia is of no commercial importance but it does provide considerable erosion protection along rivers. It is also used locally for firewood. Alders as a group are among the first species to become established on disturbed sites and many have been used in revegetation trials. Their nitrogen fixing abilities have led to their use in improving soil conditions (Tarrant and Trappe 1971).

In the AOSERP study area, *A. tenuifolia* was an important species in only two of Stringer's (1976) vegetation types. The first was the Tall River Alder-Willow Scrub (with *Salix bebbiana* and *S. lasiandra*) where no other trees were present. The second was the Bottomland Balsam Poplar Forest type. Presumably, the tree overstory was not sufficient to shade out the alder, although such may take place in time as the understory trees become more prominent. River alder was also present in one other stand, a stand of lightly forested tamarack and open muskeg, where it was common but formed less than 1% cover.

3.2.2 *Alnus crispa* (Green Alder)

Alnus crispa has a transcontinental distribution, mostly in Canada (Figure 12). Though mostly a boreal species, it extends well into the southern arctic tundra. Green alder is a spreading shrub, 1 to 4 m tall. It is a species of thickets, rocky shores, moist slopes, sandhills, borders of bogs, and open woods (Moss 1959; Scoggan 1957, 1978; McGinnies 1972), and can recover quickly after a fire (Wright 1972). As with other alders (and legumes), it forms mycorrhizal associations in root nodules with nitrogen

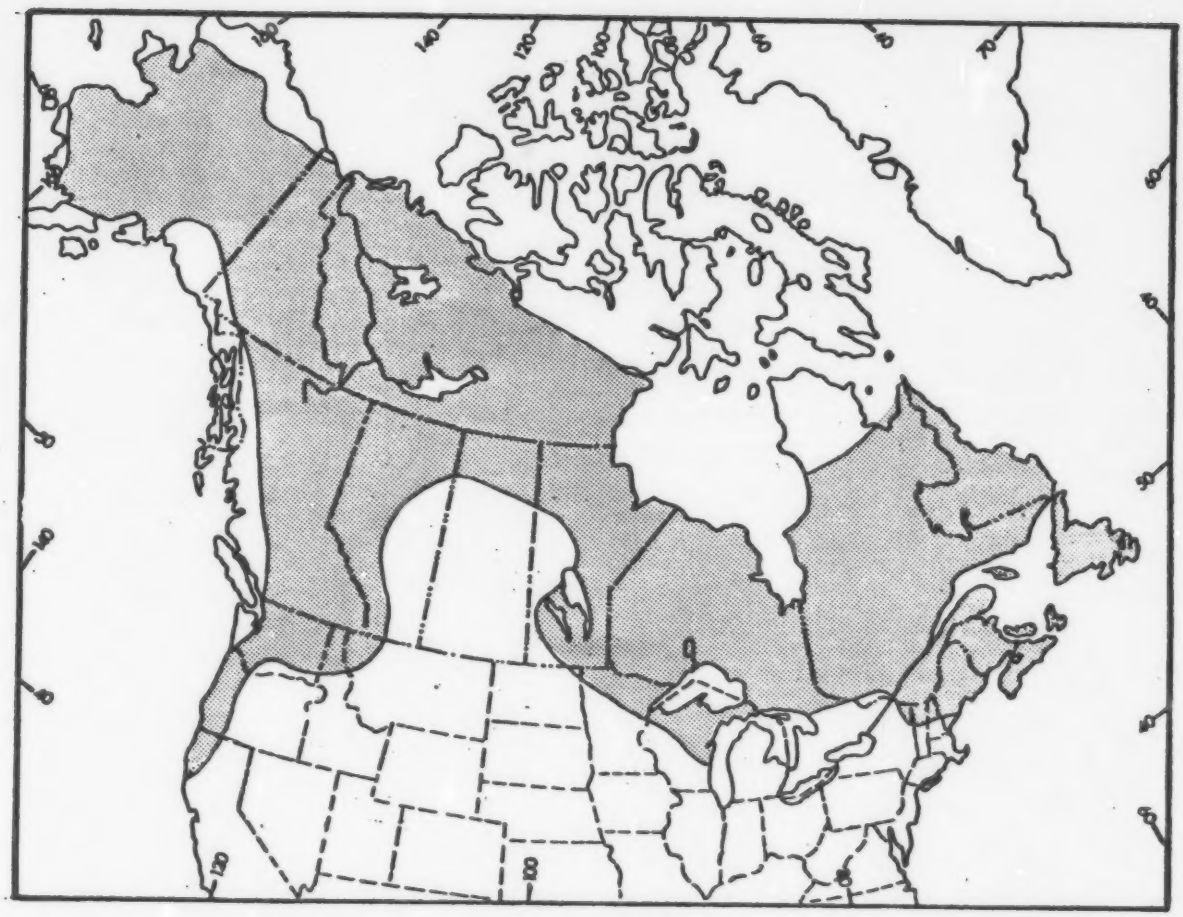

Figure 12. The range of *Alnus crispa* (adapted from Hulten 1968; Viereck and Little 1972).

fixing bacteria, thereby adding to site fertility as rootlets die and decay.

Alnus crispa flowers in spring when leaves unfold. The mature fruit ripens in the fall and seeds disperse shortly after ripening. Seeds are small, with from 1.5 to 4.0 million per kg. Of these, half or more were viable. Dormancy has been encountered in occasional seed lots (Schopmeyer 1974).

Green alder is of no commercial importance, but the twigs and buds are an important winter food for white-tailed ptarmigan and the seeds are eaten by many songbirds in fall. Its rapid regeneration after fire and the general ability of alders to be among the first plants to establish naturally have led to investigations of its suitability in northern revegetation programs. These have included seeding, cuttings, and seedling transplants on borrow pits and along roads associated with the James Bay project where it has shown some promise (Brouillette 1979). Shrub cutting trials, however, proved unsuccessful in Mackenzie Valley revegation studies (Younkin and Friesen 1976). Alders in general, including *A. crispa*, have been used to improve soil conditions (Tarrant and Trappe 1971).

In the AOSERP study area, green alder is the only tall shrub (providing 25 to 50% cover) in one cluster of Stringer's (1976) Upland Mixedwood and Deciduous Forest, and was abundant in two of the five stands in the other cluster of this type. It was also abundant (25 to 75% cover) in three of the 19 stands of the Upland White Spruce and Aspen Forest type, and present in two of five stands of the Upland Mixedwood and Coniferous Forest type. These results confirm its widespread nature in many upland boreal forest communities (e.g., LaRoi 1967a). Dix and Swan (1971) also classed it as a species with low specificity for canopy types in the Candle Lake area of Saskatchewan, although Achuff (1974) only listed it as having presence over 20% presence for the *Viburnum-Hylocomium* type of spruce-fir forest.

3.2.3 *Salix bebbiana* (Beaked Willow)

Salix bebbiana is probably the most common of tree-size willows in Canada, occurring in most forest regions (Figure 13). It occurs as a large shrub 3 m tall, or a small bushy tree 4.5 to 7.5 m tall; occasionally it reaches 10.5 m in height with a trunk 15 to 23 cm in diameter. Argus (1973) gave as its habitat: "riverine and upland forests with *Picea glauca, Betula papyrifera, Populus tremuloidea;* wet lowland thickets; *Picea mariana* muskegs; prairie margins; dry south-facing slopes; disturbed areas, such as roadsides and burns". It is one of the most common willows in forested parts of Alaska and the Yukon. In interior Alaska, it occurs as scattered individuals in most forest types, and is the most common species in thickets beside streams, swamps, and lakes; it also forms large spreading shrubs in open meadows (Viereck and Little 1972). In Alberta, it similarly is very common, growing in woods, thickets, and the borders of sloughs (Moss 1959).

Staminate and pistillate flowers are borne in catkins on separate trees, usually appearing before or with the leaves. The seeds mature within several weeks and are dispersed immediately in early summer. They are disseminated by wind or water. Trees can begin bearing seeds at 4 years of age. As many as 5.5×10^6 cleaned seeds weigh 1 kg. The seed is viable for only a few days and light is required for germination (Brinkman 1974a).

Most willow species provide browse for animals and those along rivers are useful in stabilizing banks and improving fish habitat. *Salix bebbiana* is not commercially important but, in Alaska, it is the most important producer of "diamond willow" which is carved into canes, lamp posts, furniture, and candle holders. Such "diamond willows" occur most commonly in the shade of trees or where the site is poor (Viereck and Little 1972).

In the AOSERP study area, *Salix bebbiana* is highly abundant (usually at least 25% cover) in three of Stringer's (1976) vegetation types and is scattered in isolated stands of most other types. In the Tall River Willow-Alder Scrub, it is joined in the overstory layer by *Alnus tenuifolia* and *Salix lasiandra*. In the Tall Willow Scrub, it alone forms the overstory.

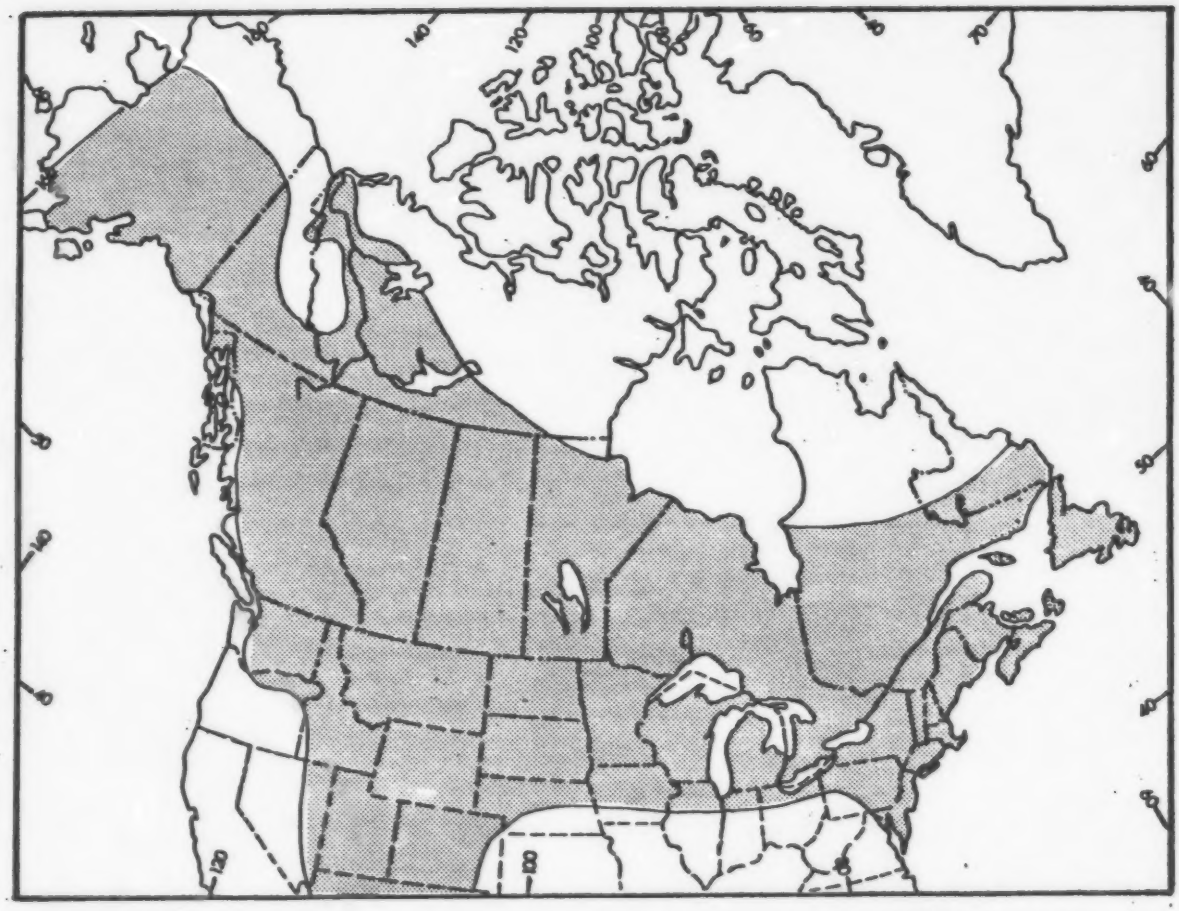

Figure 13. The range of *Salix bebbiana* (adapted from Hulten 1968; Viereck and Little 1972; Argus 1972; Scoggan 1978).

Both types are representative of large areas of tall scrub bordering rivers, and occupy wet but freely-drained depressions throughout the AOSERP area (Stringer 1976). The third type is the Lightly-Forested Tamarack and Open Muskeg. Trees are scattered and *Salix bebbiana* is a major component of the prominent shrub layer along with *Salix lasiandra*, *Betula glandulosa*, and *Ledum groenlandicum*. Dix and Swan (1971) also found *Salix bebbiana* to be of low specificity for canopy type, as it was present in most of their dominance types. La Roi (1967a) similarly listed it as present in most black spruce and white spruce-fir stands sampled largely north and west of the AOSERP study area.

3.2.4. *Prunus pensylvanica* (Pin Cherry)

Prunus pensylvanica (pin cherry) grows in most wooded parts of Canada and singly or in groves along rivers across the prairies (Figure 14). It usually is a small tree but can reach heights of 12 to 15 m and diameters of 10 to 30 cm. In moisture-deficient soils, it may be reduced to a shrub (Hosie 1973). It grows on a wide variety of sites from dry sandy soils to wet loams. In Alberta, it is common, growing in dry woods and thickets (Moss 1959).

The tree is intolerant of shade and is thus rare in the mature forest. It may often be found in clearings and on burned or recently cut-over areas (Hosie 1973) and recovers quickly after a fire (Wright 1972). It is a major successional species of most northern hardwood and boreal forest areas in eastern North America where it has a major role in maintaining overall ecosystem stability (Marks 1974). In New Hampshire, it was restricted to disturbed sites, usually greater than 0.1 ha, that had supported forest cover before disturbance, and was uncommon on abandoned pastures or old fields.

Prunus flowers are bisexual and usually appear before or with the leaves in spring. Fruits develop throughout the summer, ripening in late summer or early fall, and reach a diameter of 5 to 7 mm. Trees as young as 2 years of age may begin to bear

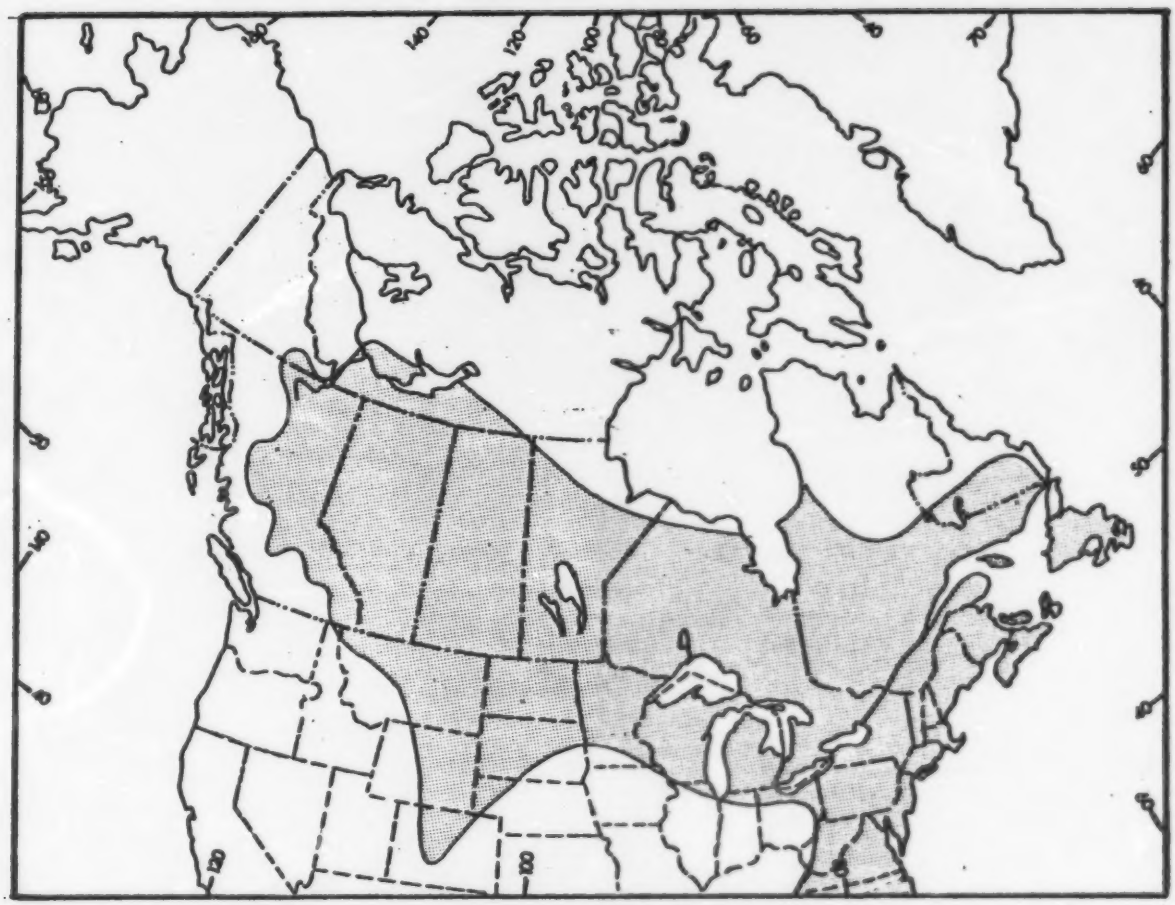

Figure 14. The range of *Prunus pensylvanica* (adapted from Hosie 1973; Scoggan 1978).

fruit. The drupe is thick and fleshy with a bony stone or pit. Fruits are eaten and dispersed by birds and animals. Well over 90% of the seed is viable. About 30 000 seeds weigh 1 kg. *Prunus* seeds have embryo dormancy requirements; a period of after-ripening in the presence of moisture and oxygen is needed to overcome this dormancy (Grisez 1974). This dormancy forms part of the species "buried seed" adaptive strategy as a rapid recolonizer following disturbance. Buried seeds may remain viable for up to 50 years and seem to germinate in response to some unknown factor(s) associated with formation of a large gap in the forest cover (Marks 1974).

The tall shrub understory was also affected downwind of the iron sintering plant at Wawa, Ontario (Gordon and Gorham 1963). *Prunus pensylvanica* was a normal component of the forest. In general, the tall shrub understory was almost wholly destroyed for 8 km out from the plant; and from 8 to 18 km out, there was much destruction. From 18 to 25 km out, tall shrubs dominated but some species showed much tip-killing. Relatively little damage was present from 25 to 32 km; beyond 32 km, the normal woodland flora was present. Some *P. pensylvanica* grew only 5 km from the plant, but none was again observed out to 15 km from the plant, beyond which point it was consistently present.

Pin cherry is of little commercial importance, being occasionally used for fuel and as a useful "nurse" tree for conifer seedlings. Other members of the genus include the cultivated stone fruits (peaches, cherries, plums) but pin cherry, though edible, is sour and is thus used for jelly making.

Prunus pensylvanica is an unimportant species in Stringer's (1976) vegetation types of the AOSERP area. It was found in only four stands. Although two of these were in the Upland Jack Pine Forest type (the type itself consisted of five stands), it is not a species distinctive of the type. The AOSERP study area is near the northern limit of this species range (Figure 14) and this may restrict its presence to the most suitable sites. It may also be more abundant on recently disturbed sites in view of its shade intolerance and successional role

(Marks 1974). Dix and Swan (1971) did not include *Prunus pensylvanica* in their list of 77 taxa with at least 20% frequency in one stand, but that may be because of its short-lived nature (about 30 years; Marks 1974) and because few recently disturbed (less than 20 years) sites were present in their study area. La Roi (1967a) listed *Prunus* spp *virginiana* and *pensylvanica* combined) as present only in stands from Alberta east. They, along with *Alnus crispa*, were usually the only low tree and tall shrub species present in Prairie province stands.

3.2.5 *Amelanchier alnifolia* (Saskatoon-berry)

Amelanchier alnifolia (Saskatoon-berry) is largely a western species, occurring west of the Great Lakes in the boreal forest and prairies (Figure 15). It is generally a shrub that may occasionally grow to tree size (Hosie 1973), reaching up to 6 m in height (Brinkman 1974b). Scoggan (1978) indicated that it grows in thickets and the borders of woods. In Alberta it is very common in open woodlands (Moss 1959). Rare in Alaska, it grows on steep, dry, south-facing bluffs, usually with aspen and common juniper (Viereck and Little 1972).

Flowers are perfect and appear in spring at about the same time as the leaves. The berry-like pome fruit ripens in late summer; each contains 4 to 10 small seeds. An average of 180 000 cleaned seeds are needed to make up 1 kg (range: 80 000 to 250 000/kg). Seed is dispersed almost entirely by the birds and animals that eat the ripe fruit. The seeds need a cold stratification period before germinating. For *Amelanchier alnifolia* seedlings, half-shade during the first year appears to be beneficial in nurseries (Brinkman 1974b).

Saskatoon-berry is important as an ornamental and the fruit is used locally for pies and jam. Numerous birds and animals also feed on the fruit (Hosie 1973). It is a suitable ornamental for interior Alaska, where it spreads freely and forms thickets.

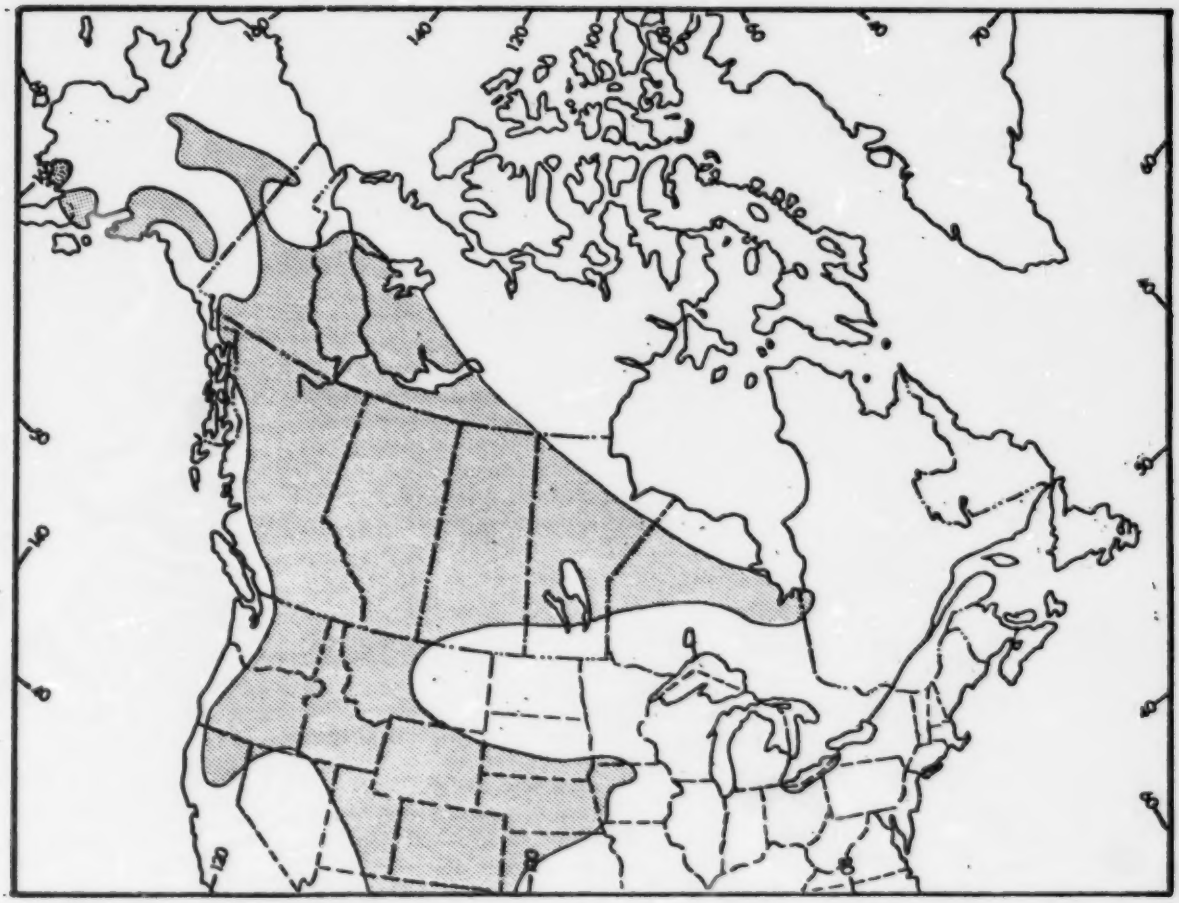

Figure 15. The range of *Amelanchier alnifolia* (adapted from Hulten 1968; Viereck and Little 1972; Scoggan 1978).

In the AOSERP study area, *Amelanchier alnifolia* occurs in only three of Stringer's (1976) vegetation types. It was present in all three stands of one of the two clusters of the Upland Mixedwood and Deciduous Forest type, but absent from all five stands of the other cluster in this type. It was also present in six of the 19 stands of Upland White Spruce-Aspen Forest type, but was rated as rare in four of the six, indicating that it is not distinctive for the type. It was also present (common but less than 1% cover) in two of the five stands of Upland Jack Pine forest. It was not listed as one of Dix and Swan's (1971) 77 taxa with at least 20% frequency in one stand. La Roi (1967a) listed it as having high regional presence in white spruce-fir stands between the District of Mackenzie and Ontario. Achuff (1974) found it in about half of his *Viburnum-Hylocomium* type spruce-fir stands in the highlands of Alberta and absent from all other types (except one stand of the *Cornus-Linnaea* type).

3.2.6 *Corylus cornuta* (Beaked Hazelnut)

Corylus cornuta (beaked hazelnut) grows in rich thickets and the borders of roads across the southern half of Canada and the northern half of the United States (Scoggan 1978; Figure 16). Its northern limit in Alberta is in the AOSERP study area (Raup 1936). In Newfoundland, it is found in thickets and clearings, on the borders of woods, banks of streams, and along shores (Ryan 1974). It is a common shrub of the northeastern United States pine-hardwoods forest where it tends to occupy mesic sites and responds vigorously following fire (Wright 1974). Where present in Alberta, it grows in thickets and open woods (Moss 1959).

It can reproduce by seedlings, sprouts, and underground stems and layers, but the most important means of recolonization is vegetative reproduction from underground stems. Although aerial stems are easily killed by even gentle fires, sprouting is prolific after spring burning and the original stand is replaced in stature and number of stems in only a few years. Repeated

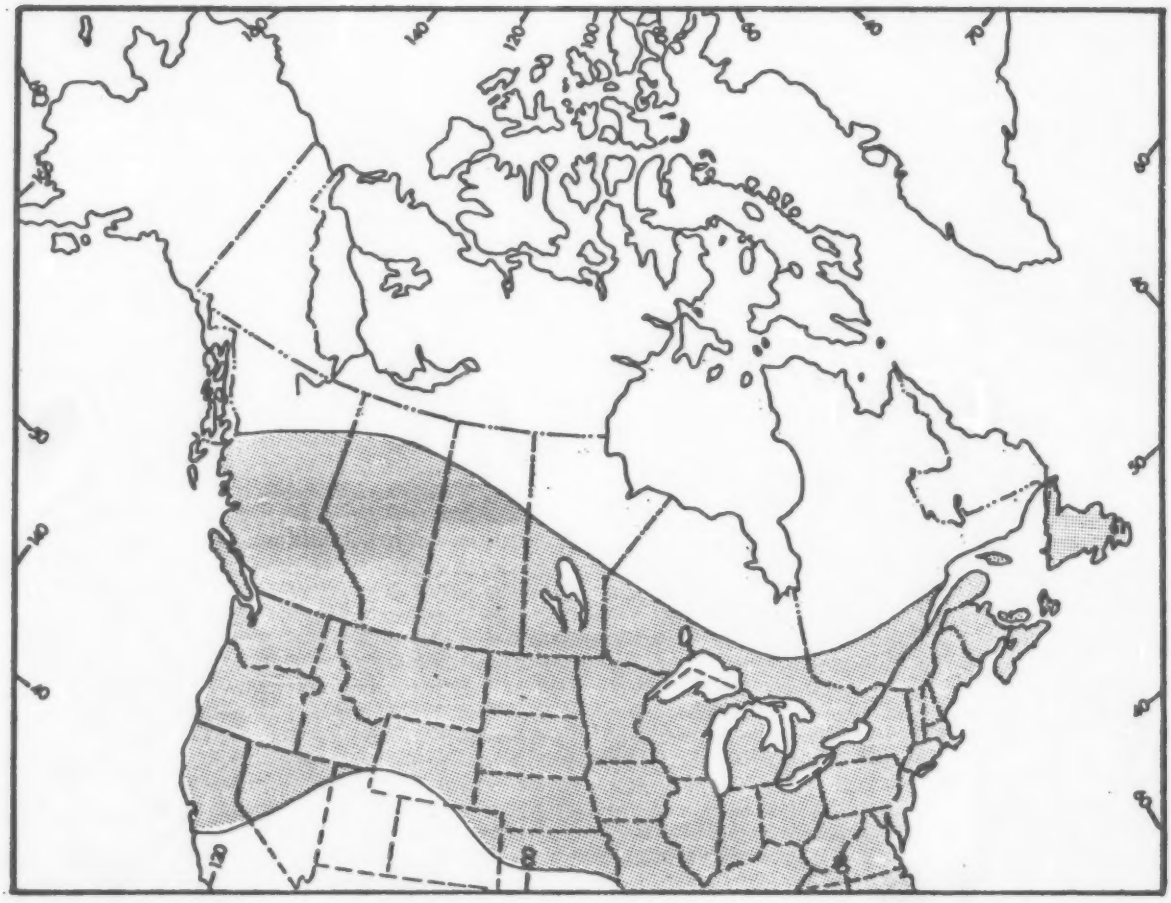

Figure 16. The range of *Corylus cornuta* (adapted from Scoggan 1978).

summer fires may destroy hazel clones. Beaked hazel is also susceptible to single hot summer ground fires that kill the near-surface rootstocks (Wright 1974).

Male and female flowers of hazel are borne separately on 1 year old lateral twigs of the same plant. Formed the previous summer, they open the following spring before the leaves appear. Fruits are round or egg-shaped, hard-shelled nuts enclosed in a husk which matures in late summer or early fall. Large seed crops are produced at irregular intervals, usually every 2 or 3 years. Natural seed dispersal is chiefly by birds or animals. About 900 to 1500 cleaned seeds weigh 1 kg. They require 2 to 6 months of prechilling before germinating (Brinkman 1974c).

Corylus cornuta was also present in the understory vegetation around the iron sintering plant at Wawa, Ontario (Gordon and Gorham 1963). It was absent within 15 km of the plant but grew consistently from there out.

Beaked hazelnut fruits are eaten by a variety of wildlife, including rodents, larger animals, and birds. A different species, *C. avellana*, is cultivated for commercial production of filberts, mostly in Europe, but *C. cornuta* is not so used (Brinkman 1974c).

Corylus cornuta is not listed as present in any of Stringer's (1976) stands in the AOSERP study area but Raup (1936) collected it near Fort McMurray and the mouth of the Firebag River. He listed it as common or occasional in upland woods.

3.3 IMPORTANT PROSTRATE SHRUBS

3.3.1 *Arctostaphylos uva-ursi* (Common Bearberry)

Arctostaphylos uva-ursi is a common evergreen prostrate shrub (7.5 to 10 cm tall) of forest and adjacent low arctic tundra areas of Canada and the northern United States (Figure 17). It often forms pure mats several metres in diameter. It grows in a wide variety of sites: exposed heathlands, rocky barrens, talus

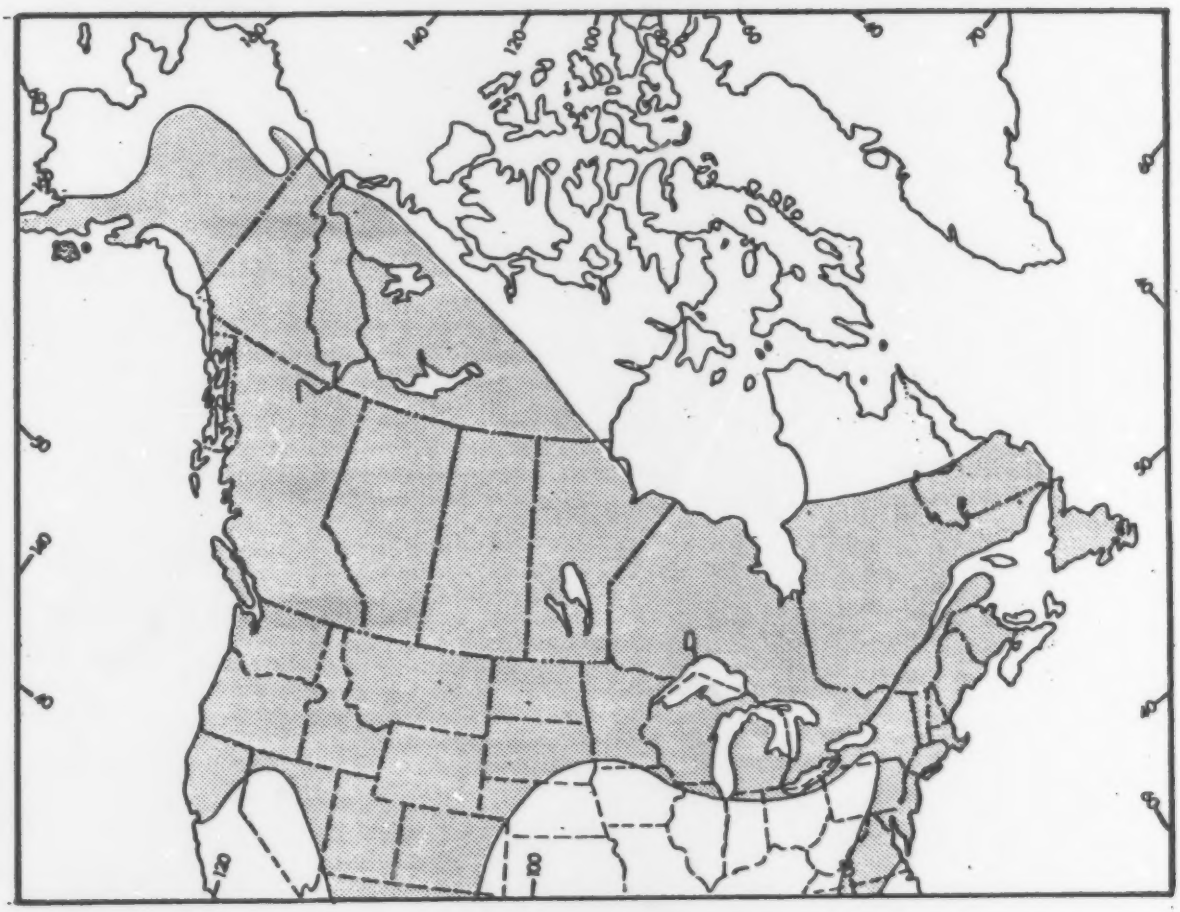

Figure 17. The range of *Arctostaphylos uva-ursi* (adapted from Hulten 1968).

slopes, and the forest floor in Newfoundland (Ryan 1974); sand-hills, rock outcrops, gravel ridges, shores, and woods in Manitoba (Scoggan 1957); open coniferous forest and gravel terraces in the Rocky Mountains (Porsild 1974); sandy and rocky ground in Alberta (Moss 1959); and dry sites in the boreal forest, usually under aspen but sometimes in open spruce stands, or on open, dry rocky bluffs in Alaska (Viereck and Little 1972).

The shrub flowers in spring and the fruit ripens in late summer to early fall. The fruit is a fleshy or mealy drupe, 6 to 15 mm in diameter containing 4 to 10 stony seeds. Up to 120 000 cleaned seeds are required to make up 1 kg. The fruits are eaten by birds and animals and the seeds are dispersed from late summer until the following spring. The seeds have hard seed coats and dormant embryos, thus requiring dormancy-breaking treatments (Berg 1974).

Arctostaphylos uva-ursi fruits are mealy, dry, and tasteless when raw but palatable when cooked. They are commonly eaten by bears (as the name implies) as well as numerous other animals and birds.

In the AOSERP study area, *Arctostaphylos uva-ursi* was virtually restricted to two of Stringer's (1976) vegetation types. In the Upland Jack Pine Forest, it was the dominant element in the sparse dwarf shrub stratum (cover in most stands was 25 to 50%). It was also present in two of the three stands of one cluster of the Upland Mixedwood and Deciduous Forest but was absent from the other cluster. Dix and Swan (1971) classed *Arctostaphylos uva-ursi* as of intermediate specificity for canopy types in the Candle Lake, Saskatchewan, area. It had relatively high presence values in jack pine stands (both tree and sapling), white spruce tree stands, and black spruce seedling stands.

3.3.2 *Vaccinium vitis-idaea* (Bog Cranberry)

Vaccinium vitis-idaea is an evergreen, creeping, mat-forming, subshrub (5 to 15 cm tall) of forest, alpine and low arctic tundra regions of Canada and Alaska (Figure 18). A widespread and common species, it grows in a wide variety of sites

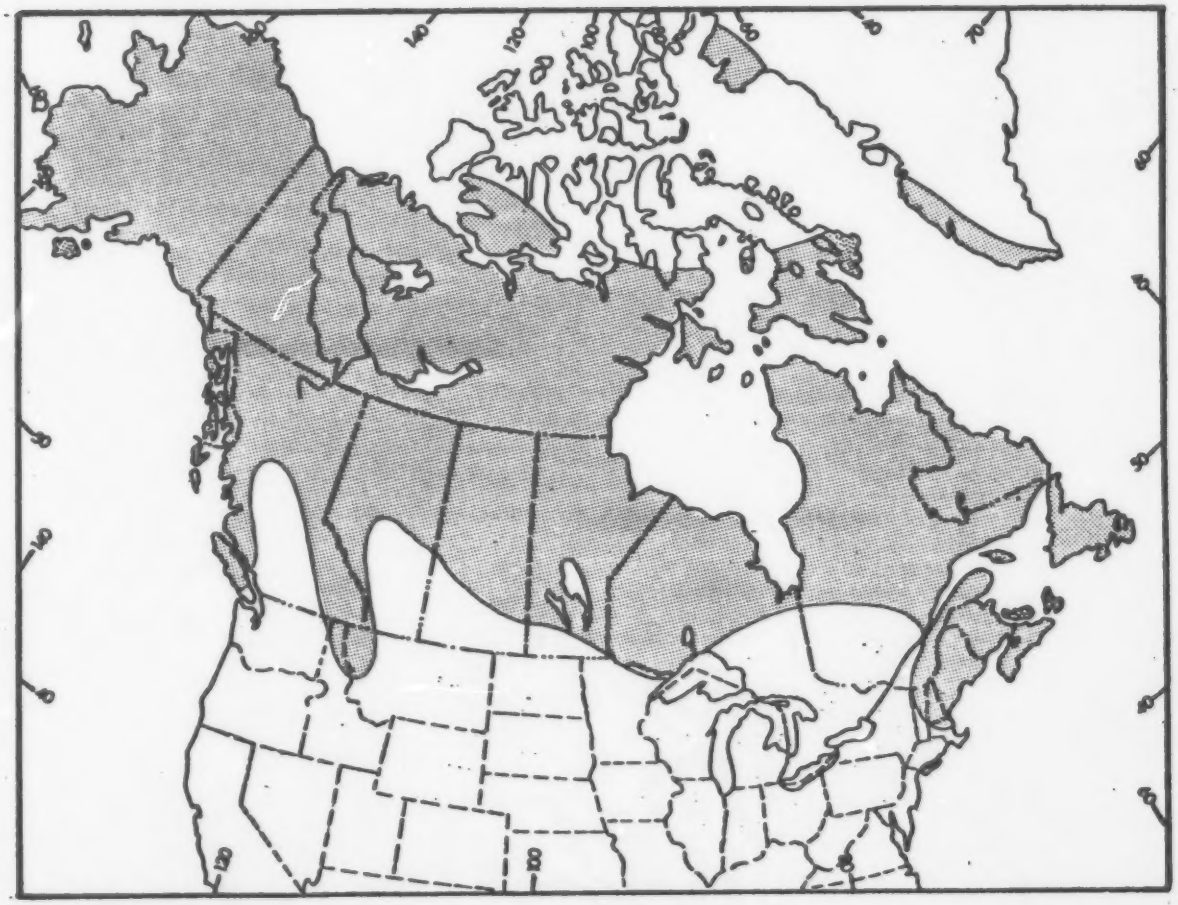

Figure 18. The range of *Vaccinium vitis-idaea* (adapted from Hulten 1968).

including spruce and birch woods of the boreal forest, bogs, and low shrub-heath and other arctic and alpine tundra types. It is found on moist, as well as dry sites, usually forming mats (Viereck and Little 1972; Moss 1959; Ryan 1974).

Vaccinium vitis-idaea flowers in early summer and the bright red sour berry (about 6 to 8 mm in diameter) ripens in late summer to early fall. The berries are abundant and usually picked in the fall after the first forest (which improves their taste). They are widely used for jellies, sauces, and jam, as well as relishes and beverages (Ryan 1974; Viereck and Little 1972). They are a food source for ptarmigan, grouse, and bears; and the foliage may also be of some value as winter browse for reindeer and caribou (Viereck and Little 1972).

Winner and Bewley (1978) found that downwind of gas processing plants in a white-spruce forest in central Alberta, *Vaccinium vitis-idaea* distribution was bell-shaped or with a peak at a localized region along the SO_2 stress gradient, indicating an increase in cover when the more dominant but sensitive species decrease.

In the AOSERP study area, *Vaccinium vitis-idaea* is present in the upland, largely coniferous, forest types and all but absent in the fen and bottomland types (Stringer 1976). In some of the upland types, it is highly distinctive and abundant. These include the Upland Mixedwood and Deciduous Forest type, the Black Spruce Bog Forest and Muskeg type, and tne Upland Mixedwood and Coniferous Forest type where it reaches 5 to 25% in many stands and up to 50% in some. Dix and Swan (1971) classified *Vaccinium vitis-idaea* as having high specificity for jack pine stands and black spruce. La Roi (1967a) listed it as present in most black spruce and white spruce-fir stands from the Prairies west.

3.4 IMPORTANT HERBS

3.4.1 *Pyrola asarifolia* (Common Pink Wintergreen) and *P. secunda* (One-sided Wintergreen)

Pyrola asarifolia and *P. secunda* are both common, low, evergreen, perennial herbs of the coniferous forests (Viereck and Little 1972; Moss 1959; Raup 1936). *Pyrola asarifolia* is largely restricted to forested areas (Figure 19) but *P. secunda* is largely restricted to forested areas (Figure 19) but *P. secunda* also extends into adjacent low arctic tundra areas of Alaska and northern Canada (Figure 20). Including the flower stalk, *P. asarifolia* is about 15 to 40 cm tall and *P. secunda* about 10 to 25 cm tall. Each stalk bears 8 to 15 or more flowers. The fruit is a five-parted dry capsule with many small seeds. Flowers appear in June and July (Viereck and Little 1972; Vance et al. 1977).

Winner and Bewley (1978) found that the distribution of *Pyrola asarifolia* in a spruce forest downwind of a gas-processing plant emitting SO_2 tended to decline at a constant rate, indicating sensitivity to SO_2.

In the AOSERP study area, each species is present as common (but with less than 1% cover) in the highly diverse shrub stratum of about half the stands of the Upland White Spruce-Aspen Forest type (Stringer 1976). Both occur together in four stands. Both species are virtually absent from other stands; *P. asarifolia* occurs in four other stands, *P. secunda* in only two. Dix and Swan (1971) listed *P. asarifolia* as highly specific for canopy types, particularly aspen (both trees and saplings) but also for birch tree stands. They did not list *P. secunda* in their 77 taxa having 20% frequency in at least one stand. La Roi (1967a) found *P. secunda* virtually throughout Canada in both black spruce and white spruce-fir stands; *P. asarifolia* was common but restricted west of Manitoba in white spruce-fir stands. Achuff (1974) listed *P. asarifolia* in all *Viburnum-Hylocomium* type spruce-fir stands and in four of five *Cornus-Linnaea* type stands on highlands of northern Alberta. *P. secunda* was present in at least half the stands of all four types.

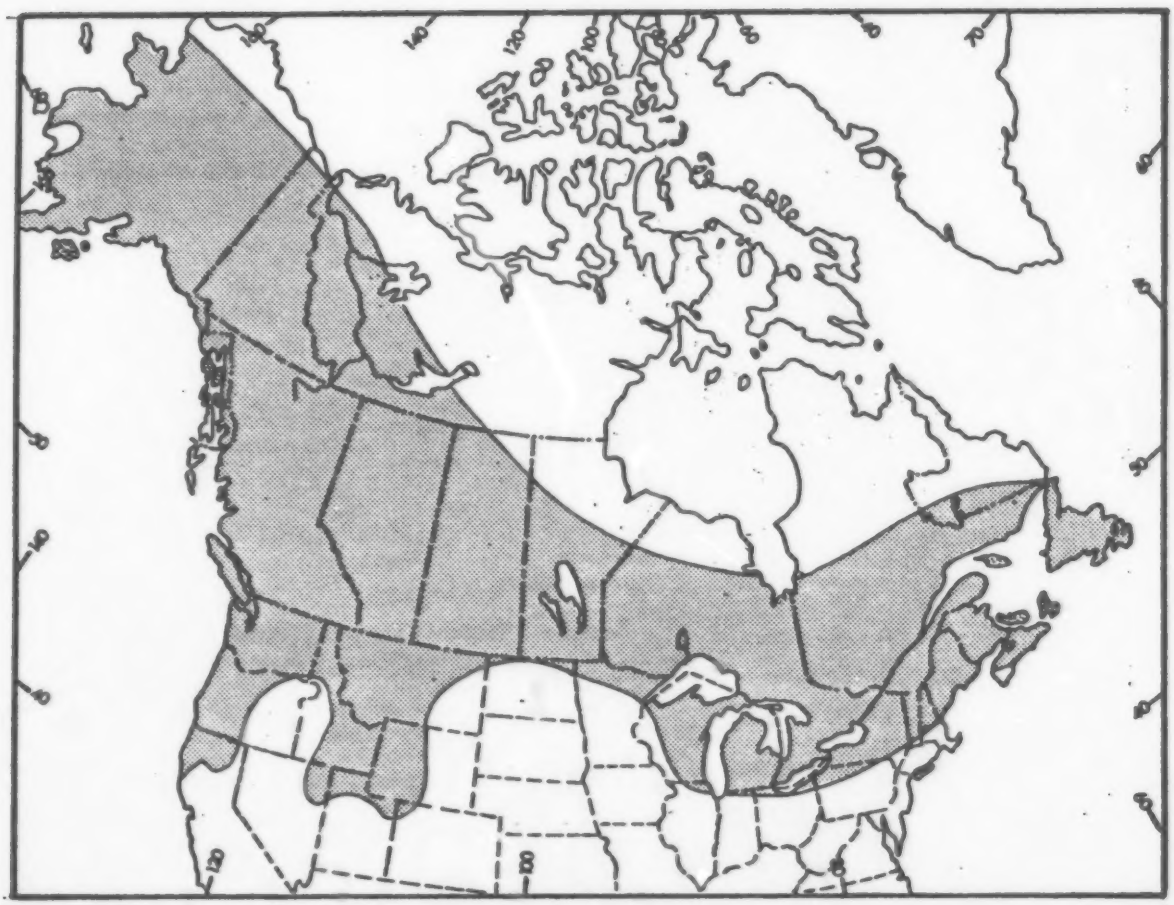

Figure 19. The range of *Pyrola asarifolia* (adapted from Hulten 1968).

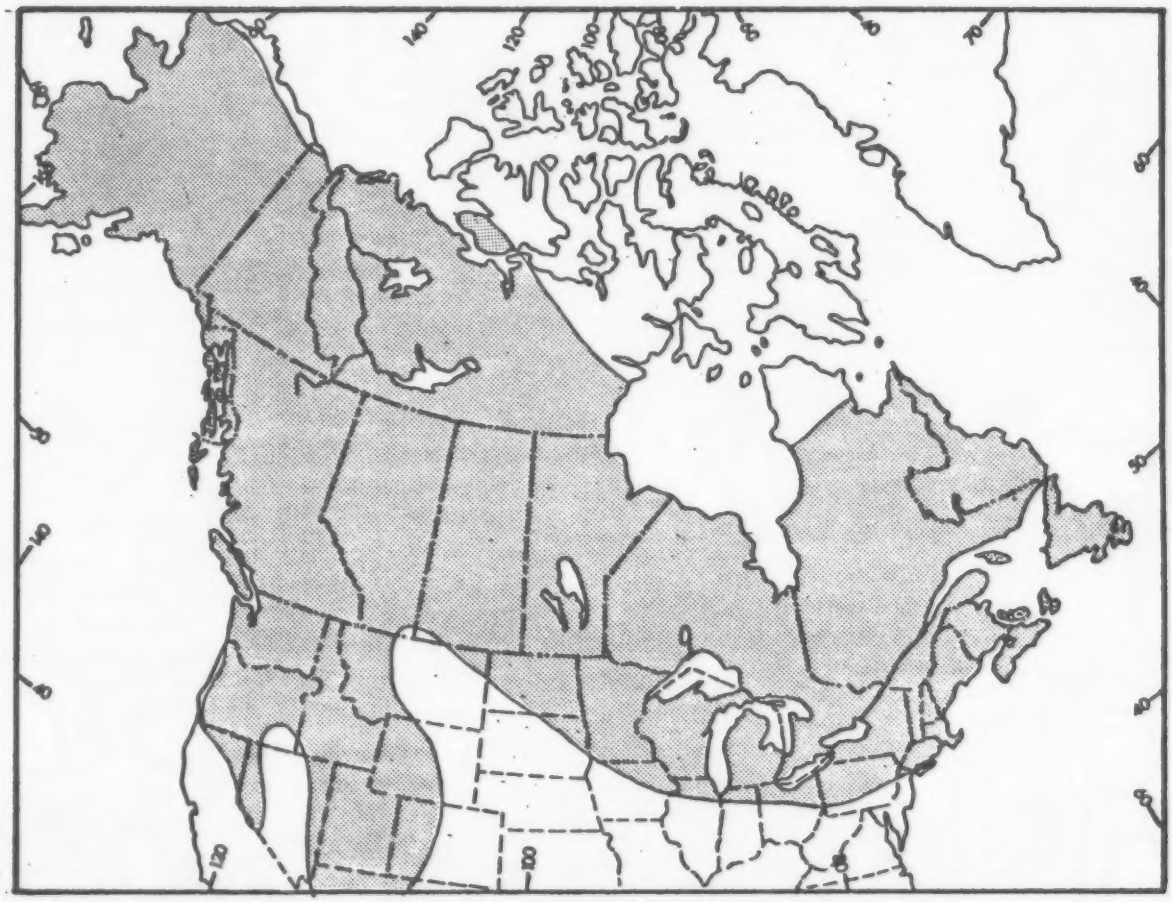

Figure 20. The range of *Pyrola secunda* (adapted from Hulten 1968).

3.4.2 *Aralia nudicaulis* (Wild Sarsaparilla)

Aralia nudicaulis is a perennial herb, about 30 to 40 cm tall. The plant is a characteristic feature of the understory of rich woodlands in Alberta (Moss 1959) and parkland groves and wooded ravines of the prairies (Vance et al. 1977); it grows in woods, thickets, gravel ridges and rock outcrops in the southern three-quarters of Manitoba (Scoggan 1957). It is found across most of Canada, flowering in late spring to early summer.

Of the four in this section, *Aralia nudicaulis* was the only herb present in the ground flora of the vegetation around the iron sintering plant near Wawa, Ontario (Gordon and Gorham 1963). In general, the ground vegetation was mostly destroyed for 8 km out from the plant. From 8 to 18 km out, the ground flora was dominant although floristic variety declined. Between 18 and 25 km, the normal number of species was present and showed relatively little damage. Beyond 25 km, the normal woodland ground flora was present. Some *Aralia nudicaulis* was present 10 km from the plant, but none was again observed until 15 km from the plant, beyond which it was consistently present.

In the AOSERP study area, *Aralia nudicaulis* is one of the dominant species of the dwarf shrub-herb stratum of the Upland White Spruce-Aspen Forest type (Stringer 1976). It was present in about two-thirds of the stands of this type and had 25 to 50% cover in many of these. It was also present in two of the five stands of Bottomland Balsam Poplar Forest (cover 5 to 25%) and it was prominent (5 to 25% cover) in two of three stands in one cluster of Upland Mixedwood and Deciduous Forest. Dix and Swan (1971) found it to be highly specific for aspen stands (both tree and sapling) and birch (tree) stands in the Candle Lake area of Saskatchewan. La Roi (1967a) found *A. nudicaulis* present in most white spruce-fir stands between the Northwest Territories and Nova Scotia and in most black spruce stands between Alberta and Ontario. Achuff (1974) found it in all or almost all stands of three types of spruce-fir forest on high-

lands of northern Alberta, (the *Cornus-Linnaea* type, the *Viburnum-Hylocomium* type, and the *Calamagrostis canadensis* type).

3.4.3. *Lathyrus ochroleucus* (Peavine)

Lathyrus ochroleucus is a legume. It grows in moist woods, thickets, and clearings from Quebec west (Scoggan 1978). In Alberta, it is very common among bushes, in open woods, and in northern meadows (Moss 1959; Raup 1936). Vance et al. (1977) described its habitat in the prairies as including margins of aspen groves and relatively open areas inside them. It is a perennial vine climbing to a length of 30 to 90 cm. Flowers appear throughout the summer, 12 to 20 in each cluster. The fruit is a dry, thin-walled pod about 5 cm long, containing four to six seeds which are considered poisonous (Vance et al. 1977).

In the AOSERP study area, *Lathyrus ochroleucus* was restricted to 12 of the 19 stands of Upland White Spruce-Aspen Forest (and one other stand) where it was considered one of the lesser dominants of the diverse dwarf shrub-herb stratum (Stringer 1976). It was common but contributed less than 1% cover. Dix and Swan (1971) classed it as highly specific for deciduous upland forest types in the Candle Lake, Saskatchewan area. It was most frequent in aspen stands (tree and saplings) and tree stands of birch or poplar. La Roi (1967a) listed it as having high regional presence for white spruce-fir stands in Alberta and Saskatchewan since it was absent elsewhere. It was present in about half the black spruce stands across the Prairies. Achuff (1974) reported it consistently (in 11 of 15 stands) only in spruce-fir stands of the *Viburnum-Hylocomium* type in highlands of northern Alberta.

4. VEGETATION DYNAMICS IN THE BOREAL FOREST

Details on the vegetation dynamics of the AOSERP study area are not available, with the exception of the Athabasca Delta area. There is, however, a great deal of information on the recovery after fire and related successions in other similar boreal forest areas. They should not be taken as describing what will happen in the AOSERP study area but should be used as an indication of what could happen and as a reference point against which ultimately observed changes can be compared.

The term "succession" is used in this report to mean observed change-over through time without implying a pre-determined end point. (The reasons for this are discussed in Section 5.1 "Communities, Climax, and Succession - A Brief Review").

4.1 THE ROLE OF FIRE

There seems to be general agreement that the boreal forest in the AOSERP study area is a fire disturbance forest. Succession after fire, in addition to being complex, appears to be unpredictable. Ahlgren and Ahlgren (1960) noted that "very few generalizations can be derived from the literature concerning plant succession following fire, since so many conditions in addition to the actual burning come into play as factors in the process". Post-fire succession in British Columbia varied in its course and rate, depending on pre-burn vegetation, microclimatic variability, soil conditions, and available seeds (McMinn 1951). In addition to fire intensity, frequency and nature are equally important, as is post-burn weather for several years after fire.

4.1.1 Evidence of Fire

Rowe (1970) noted an almost universal occurrence of charcoal in northern forests soils, and Lutz (1956) concluded that extensive fires occurred in Canada, Alaska, and northern Europe. Swain (1973) reported charcoal dating back 1000 years in Minnesota, with evidence of fires occurring on a 20 to 100 year basis.

Heinselman (1973) documented a 400 year fire history on the Boundary Waters Canoe Area of Minnesota. Even with periodic fires, the pollen diagrams remained virtually the same, indicating a persistence of the principal species and perhaps competition among them.

In the last 500 years, a major fire occurred about every 80 years in the Great Lakes region of Ontario (Cwynar 1978). Pollen analysis indicated very little compositional change for 1200 years, suggesting that fire is a natural phenomenon affecting the vegetation.

4.1.2 Causes, Extent, and Frequency of Fire

Prehistorically, the major cause of fire in the boreal forest was almost certainly lightning, and it continues to be the major cause today. Approximately 72% of fires in northern Saskatchewan on caribou winter range were lightning-caused (Scotter 1972). Essentially all of the area burned and 85% of the fires reported south of the Great Slave Lake were lightning-related (Johnson and Rowe 1975). In the Yukon, 76% of the fires were lightning-related (Requa 1964), while farther east in the Mackenzie Valley, 97% of the area burned from 1971 to 1974 was attributed to lightning (Rowe et al. 1975).

Primitive man used fire as a management tool in the northern forests. Indians in Alberta regularly set fires to improve wildlife habitat, reduce fire hazards in and near camps, assure supplies of dry firewood, and dry out and clear trails through muskeg (Lewis 1977). This practice continued almost up to the present day. Although these fires were set as controlled burns, they undoubtedly sometimes got out of control and burned extensive areas.

More recently, man's activities can be a major contributing factor to fire in central Alberta (Kiil and Grigel 1969). During May 1968, a dry, windy period combined with fire-assisted land-clearing practices inadvertently caused 250 fires which

burned 380 000 ha of forest over a 15 day period. Scotter (1964) showed a strong correlation between man's activities and increased fires in northern Saskatchewan, a threefold annual increase in area burned between 1945 and 1959 compared to the 1840 to 1888 period. Between 1940 and 1969 in Alaska, about 70% of the fires were man-caused but they only accounted for 21% of the area burned (Barney 1971a, 1971b; Barney and Comiskey 1973).

Year-to-year variation in area burned for any particular region is high. During a 5 year period, fire destroyed 2% of Wood Buffalo National Park, an area where fire suppression is practiced and human access is limited (Kelsall 1968). In the area between Great Slave and Great Bear lakes, approximately 27% of the forest burned over in a 20 year period (Kelsall 1957). Both areas are in or near high potential fire risk areas (Simard 1973). Johnson and Rowe (1973) calculated that the studies by Scotter (1964) showed that approximately 1% of the total forest area burned per year. No trees older than 120 years grew in 89 stands sampled in central Saskatchewan, indicating maximum probable time between burns (Dix and Swan 1971).

Fire risk in the North increases as the stand ages (Rowe et al. 1975). The recent rash of fires in the Mackenzie Valley may be due to forests reaching maturity following a similar period of fires in the 1800's (Rowe et al. 1974). Age alone, however, does not affect increased fire risk; site conditions, particularly moisture, are of equal or greater importance.

The conditions favorable for fire are much more likely to occur on upland slopes and other sites with coarse textured soils, which encourage drought and lower humidity. The fuel buildup of dry material, the lack of a lush shrub layer, and the usual increased proportion of coniferous trees would increase the susceptibility of the mature upland forest to fire (Rowe et al. 1975). The most frequently and intensely burned areas are uplands and upland ridges, particularly if oriented in the direction of prevailing winds (Heinselman 1973). Wetlands, other lowlands, and

lower slopes of high ridges burn less frequently or intensely depending on orientation and location relative to lakes, streams, and other drainageways.

Lightning-caused fires are numerous, occur over a very wide area, and profoundly affect the vegetation mosaic. Taylor (1969) estimated that if the 8×10^6 daily lightning strikes were evenly distributed, about 500,000 would strike in the 3×10^9 ha of forest land. Only a small percentage of strikes start fires, most of which are small and self-extinguished. Scotter (1970) found 60% of the fires in the subarctic forest burned less than 4 ha, and Rowe and Scotter (1973) reported that 88% of northern and 82% of southern Saskatchewan fires during an 8 year period burned 4 ha or less.

In northern Minnesota, "significant fires" occurred in 1 to 8 year intervals between 1739 and 1926, whereas before and after that period, intervals between fires were greater (Heinselman 1973). Major fires, those burning more than 250 km^2 (6% of the virgin forest), occurred at much longer intervals, and most of the total area affected was burned during major fire years.

4.1.3 Fire Characteristics

The effects of fire are directly related to the type of fire. Wright and Heinselman (1973) recognized five types of fire: (1) long-interval crown fires; (2) short-interval crown fires; (3) long-interval surface fires; (4) short-interval surface fires; and (5) all possible combinations of these four. Crown fires driven by high winds kill most of the trees but cause little damage to the moss and humus layers. A slow intense fire kills the trees, the understory, and the moss mat (Raup 1946).

The effects of fire are also determined by the species composition of the forest. Jack pine and lodgepole pine stands have a high crown and surface fire hazard during all seasons. Black and white spruce and balsam fir will readily crown during dry weather, but surface fires are relatively hard to start.

Aspen, birch, and tamarack, which have a high surficial fire hazard in the spring except for unusually dry periods, have a very low crown fire hazard (Rowe and Scotter 1973). The greater the proportion of conifers in mixedwood stands, the greater the fire hazard.

4.1.4 Effects on Soil Surface

The effects of fire on the soil are highly variable and relate to site conditions. Fires in the North usually consume only a portion of the surficial organic materials and do not expose much mineral soil (Kelsall et al. 1977). Lutz (1956), however, reported that 30 to 40% of the mineral soil could be exposed on burned areas. On burned islands of Great Slave Lake, exposed mineral soil was totally removed by erosion (Kelsall 1968). The complete destruction of the humus layer often occurs on well-drained and/or rocky sites or ridges leaving the soil exposed (Lutz 1960). This may not lead to serious erosion as erosion and runoff after fire are minimal in northern areas (Viereck 1973). Fire rarely has any effect on soil structure or texture (Lutz 1960).

4.1.5 Soil Temperatures and Permafrost

Fires also modify soil temperature regimes. When forest cover is removed by fire, heat enters the soil more readily in summer and is retained longer in winter because of the insulating effect of snow cover. The resulting net gain during the year (as compared to a forested area) results in a warmer soil for many years. This is of great importance in slowing down or reversing the well-documented trend of increasing litter accumulation with increasing latitude (Bray and Gorham 1964). Soil temperatures are colder in southern forest openings than under trees (Komarek 1971). The reverse is true in northern forests, primarily because conifers shade the ground in summer and promote the build-up of decomposition-resistant organic layers, minimizing heat flow into the soil. During winter, conifers can readily intercept snow,

preventing the development of an effective soil insulating snow cover. The combined effect is a cold soil much of the year.

Kershaw and Rouse (1976) examined burns ranging from 0 to 81 years of age north and east of Lake Athabasca. Surface temperatures were immediately raised 60 to 70% after a burn. Twenty-four years after a burn, summer surface temperatures remained 30 to 40% higher than adjacent areas.

Although there are few, if any, extensive areas of permafrost on the AOSERP study area, the northern half lies on the fringe of discontinuous permafrost (Klohn and Davison 1978). The effect of fire on permafrost varies with site, type of permafrost present, geographic location, substrate, slope, and amount of surface organic material remaining (Sykes 1971; Crampton 1973). Medium-to-fine textured soils often undergo subsidence with increased thawing, but coarse-textured soils remain relatively stable (Rowe et al. 1974). The active zone of permafrost areas increases after fire (Bliss and Wein 1971; Kershaw et al. 1975; Rouse and Kershaw 1971, Heginbottom 1973; Cody 1965). Wein (1971) and Mackay (1970) reported a 30 to 50% increase of the active layer within 2 years following fire. Burning, however, does not always thicken the active layer. Viereck (1973) found a decrease in the active layer (47 cm versus 44 cm) on unburned sites in four burned black spruce stands at the end of summer after a June fire near Fairbanks, Alaska. The thickness of the active layer decreased several years after a fire near the northern tree-line in Russia due to the increased growth of *Eriophorum* spp. which resulted from increased moisture (and probably nutrients). This effectively insulated the ground. The colder, wetter soil which resulted prevented the re-establishment of trees and created pyrogenic tundra (Kryuchkov 1969).

Zoltai and Pettapiece (1973) considered the most important function of vegetation to be insulation. Removal of the surface layer may increase thickness of the active layer more than fire (Brown 1970). The active layer in black spruce stands near Inuvik was 9 cm greater in burned areas and 35 cm greater where the organic layer was removed (Heginbottom 1971).

4.1.6 Effects on Available Nutrients

Increased soil temperature affects soil nutrients, particularly in frozen soil. In frozen Alaskan soils, most nutrients (particularly calcium, potassium, and nitrogen) are bound in the lower organic portions, which remain frozen and unavailable (Heilman 1966, 1968). Increasing the depth of the active layer releases these for plant use. Foliar nitrogen decreased and potassium and phosphorus deficiencies occurred in the later stages of succession to a black spruce-sphagnum stand as the active layer decreased (Heilman 1966).

Fire also makes large amounts of minerals and trace elements available in the ash. Available calcium, nitrogen, phosphorus, and potassium increased at the soil surface for up to 5 years following a burn (Lutz 1960; Kelsall et al. 1977; Wein and Weber 1974; Ahlgren 1960, 1970; Scotter 1971). Under intense fires, nitrogen and potassium are volatilized and lost (Behan 1970).

The release of mineral nutrients stored in Kayll's (1968) "frozen assets", including those in standing biomass and litter, can amount to 680 t/ha in some locations (Kiil and Grigel 1971). Although total nitrogen decreases when the litter is burned, the amount available for recycling is increased (Kelsall et al. 1977; Lutz 1960). Total nitrogen levels may increase after burning due to an increase in nitrogen fixing bacteria (Tamm 1950).

4.1.7 Effects on pH

Increases in surface and subsurface pH have been noted after fire (Armson 1969; Kayll 1968; Kershaw et al. 1975; Scotter 1963). Behan (1970) considered the increase (more notable under conifer burns) as being beneficial to the establishment of seedlings of most plants. Increased pH along with the increased soil temperature produces much more rapid decomposition of not only the remaining litter and organic material but also the slash which falls for many years after the burn.

4.2 SUCCESSION

Whether a mature, self-perpetuating community exists in the boreal forest of west-central Canada and what it might consist of, for the most part, are academic questions. Few if any areas remain unburned for a sufficient time to allow development of late successional stages (Bloomberg 1950; Horton 1959; Rowe 1961). Dix and Swan (1971) concluded that in the forests at Candle Lake, Saskatchewan, burning has been so frequent the terminal community is impossible to determine.

Rowe (1961) and Dix and Swan (1971) were of the opinion that balsam fir is the only species able to continually reproduce itself under a closed canopy. Rowe (1961) added, however, that even though it can reproduce, balsam fir is of only minor importance due to its relatively poor adaptation to the dry continental conditions of the interior. He stated that "decadent forests do not return through an inevitable cycle to youth and an optimum phase but rather tend to remain open, unhealthy, ragged, and frequently brush filled, awaiting the rejuvenating touch of fire, flood, or windfall-ploughing of the soil." In spruce-fir forests to the west of the AOSERP study area, Cormack (1953), Moss and Pegg (1963), Beil (1966), and Day (1972) considered spruce-fir communities to be self-perpetuating. Their observations, however, were associated with different species and higher elevations or mountainous terrain which are more favorable to fir due to better moisture conditions (Rowe 1961). Although specifics may not apply to the AOSERP study area, the general evidence from both cordilleran and spruce-fir forests may be used to evaluate succession in spruce-fir forests (Achuff 1974).

4.2.1 Muskeg and Related Terrain

Perhaps the least understood and the most variable and complex vegetation dynamics occur in the muskeg and related types including bog and fens. Sjors (1961) stated that "succession on peatlands includes much more than the normal successions starting in a wet habitat that are described in ecological textbooks".

Traditionally bog succession has been viewed as invasion of depressions by bog mosses forming muskeg and eventually bog forests. Moss (1953a, 1955) and Raup (1935) viewed bog succession as terminating in this manner. On shallow depressions and level terrain, grasses and sedges may be invaded by *Sphagnum* and other mosses although there is no deep accumulation of peat. Several *Salix* and *Betula* species are often present. Eventually they may be replaced by the black spruce-feather moss association (Moss 1955). In turn, given sufficient time, this could probably be replaced by white spruce forest, but it usually is maintained by poor drainage and periodic burning (Moss 1953a).

On deeper depressions, open water may be colonized by *Drepanocladus* spp. and later *Sphagnum* spp. leading to the acid bog stage with considerable accumulation of peat. Moss (1953a) reported the following sequence of *Sphagnum* species as site conditions became progressively drier: *S. subsecundum, S. recurvum, S. magellanicum, S. capillaceum*, and *S. fuscum*. The later, dry stage is conducive to invasion by scattered tamarack, paper birch, and clumps of *Salix* spp. and *Betula* spp. Moss (1955) felt that the resulting black spruce-peat moss association would develop into a black spruce-feather moss association, but disturbance by fire usually prevents this. This is the sequence he considered as the chief mode of bog development in northern Alberta.

A third type of bog, open and sparsely treed, is also present in the region. It may result from a *Drepanocladus-Carex* community forming in basins following an aquatic vegetation stage. If the water table remains high and the area wet, a change to a tamarack association often occurs, since these wet, open conditions favor that species. Eventually it would change to the *Sphagnum-Ledum-Picea* type as *Sphagnum* mounds grow. The drier microhabitat presented by these mounds is favorable to black spruce which will replace tamarack due to the latter's shade intolerance. Again, given sufficient time, the black spruce-feather moss type would prevail (Moss 1955).

Retrogression in bogs has been described and attributed to changes in climate, fire, a raising of the water table, or a decline in nutrient status as peat accumulates (Lewis and Dowding 1926; Jeglum 1968; Sjors 1961). The degree of retrogression depends on the nature, intensity, and extensiveness of the disturbance. Sjors (1961) noted an expansion and joining of pools in the Hudson Bay lowlands, with the sites becoming even wetter. The same phenomenon occurred in Saskatchewan (Jeglum 1968). Sjors (1961) concluded "rather than leading to uniformity the paludification and further changes have increasingly diversified the habitats and their vegetation".

Muskeg and associated wetland types are highly variable in other parts of Alberta (Lewis and Dowding 1926; Lewis et al. 1928 Moss 1953a). Stringer (1976) felt such areas were so variable that they could only be evaluated on a site-by-site basis and Jeglum (1968) concluded that the interaction of succession and environmental gradients was so complex that detailed studies of permanent quadrats were required.

4.2.2 Rivers and Lake Shores

Vegetation along streams characteristically occurs in bands with increasing distance from the water. On the AOSERP study area, these bands are most prevalent along the meandering Clearwater River and on the Lake Athabasca Delta.

Two detailed studies have been carried out, one in Wood Buffalo National Park (Raup 1935) and the other on the Athabasca Delta (Dirschl 1973). Raup (1935) developed successional sequences for six habitat types: local river deposits, delta plains, partially ponded creeks, ponded creeks, isolated sloughs, and saline sloughs. Dirschl (1973) described references for four habitats (sites) on the Athabasca Delta: flowing channels and river deposits, lake shores and delta plains, ponded channels and perched basins, and meander scrolls and back swamps. Sequences presented by the two authors were similar.

Aquatic plants are usually missing from deposits in channels and rivers because of the flowing water. Raup (1935) felt that the early stages were controlled by soils and their configuration and by stream current characteristics. The successional sequence included a community dominated either by *Equisetum fluviatile* or *Eleocharis-Glyceria* (Dirschl 1973). This is invaded by *Equisetum pratense* and *Salix interior* which gives way to a willow community of *Salix discolor* and *S. bebbiana*. Eventually balsam poplar apparently replaces *Salix discolor*. In time, it would develop into a white spruce-balsam fir community.

Dirschl (1973) concluded that "succession in the Delta does not follow a single pathway but takes the form of a branching network in which various species or species groups may dominate in different locations during the same seral stage and fuse during succeeding stages". He noted this was particularly true during the shoreline and meadow stages. Reasons for this "patchwork" of type within a seral stage may be seed supply and minute differences in moisture and nutrient status. He speculated that under conditions of no disturbance, it would take approximately 110 years to reach to coniferous forest stage.

The lakeshore and delta plains site may follow a number of pathways (Dirschl 1973). All sequences apparently start with a *Potamogeton* stage followed by a *Senecio-Scirpus* stage. This may be followed by either an *Eleocharis palustris* or *Beckmannia-Scolochloa-Carex* stage. These can be followed by a wet meadow community including *Carex atherodes* and *C. aquatilis*. Other communities may include *Phragmites communis* and *Calamagrostis canadensis*; the former follows *Eleocharis palustris*, the latter the *Carex* spp. All of these give way to a *Salix planifolia-S. mackenzieana* stage which is followed by the *Salix discolor-S. bebbiana* community which proceeds as described above.

On ponded channels and perched basins, the initial stage is a *Potamogeton-Nuphar* type (Dirschl 1973). This is followed by *Senecio* or *Typha* types, then the *Scirpus-Glyceria*, which gives way to *Eleocharis palustris* and *Carex* spp. The next type is *Carex*

atharodes and *C. rostrata* and later *Calamagrostis canadensis* dominates, after which the sequence proceeds as above.

For meander scrolls and back swamps, the initial aquatic communities include *Potamogeton* or *Potamogeton-Nuphar* and later *Myriophyllum-Ranunculus*. These are replaced by *Scirpus-Typha* which gives way to a *Carex rostrata-Potentilla palustris-Acorus calamus* or a *Phragmites communis* type. *Salix pedicellaris-Menyanthes trifoliata* then follow. They may then go through a bog development to a black spruce and tamarack forest.

4.2.3 Uplands

The upland forests are the most disturbed of the boreal forest communities. On sandy sites and other coarse textured sites, jack pine is usually dominant. On the drier sites, burning results in rapid release of seed from the serotinous cones. The seed germinates and seedlings quickly recolonize the area and redevelop the pine-heath type (Moss 1955). This type is characterized by an open stand which may be gradually and partially filled in by drought-resistant species such as *Arctostaphylos uva-ursi, Vaccinium vitis-idaea, Elymus innovatus, Oryzopsis pungens, Polytrichum* spp., and *Cladonia* spp. (Moss 1953b). Moss concluded that this type would be able to maintain itself and not be replaced by white spruce because of the xeric conditions and the recurrence of fire which repeats the cycle. In the Lake States, however, fire a second time before saplings can produce cones will eliminate jack pine stands (Eyre and LeBarron 1944). These areas often revert to shrub or grass types which would offer severe competition to the establishment of other trees.

Raup (1946) tentatively mapped vegetation on the upland areas between the Richardson River and Lake Athabasca on the east side of the Athabasca River. This area roughly corresponds to the Athabasca Plain physiographic area (Figure 2). In the Lake Athabasca area, stands containing jack pine ranging from a few years up to 120 years of age can be found. There was no evidence

of compositional changes over a long time period with the repeated fires (Raup 1946).

On mesic upland sites with heavier soils, white spruce is reported as the successional end point when it escapes fire (Raup 1946; Moss 1953b, 1955; Stringer 1976). In the Athabasca-Great Slave Lake region, a wind-driven fire through a spruce forest kills most of the trees, doing little damage to the humus and moss layer (Raup 1946). The stand returns to spruce immediately, with occasional pine, aspen, and balsam poplar. A slow intense fire, however, kills the spruce (both trees and seedlings) and is followed by pure aspen stands or an aspen-pine mixture. Aspen being shade intolerant is not able to reproduce itself; in dense stands it gives way to balsam poplar and later white spruce.

Raup (1946) also noted that on xeric sites with intense burns the vegetation may be completely destroyed. The resulting pure stands of jack pine are replaced with a pure spruce forest or with interpolation of aspen and balsam poplar. He stated that in the region, based on earlier burn evidence "a commonly observed forest type is one of young vigorous spruces mixed with a scattered stand of decrepit and tottering old jack pine."

Moss (1955) had a somewhat different view of fire-initiated succession. Light fires which only burn the surface of the humus layer stimulate the growth of shrubs and herbs and the suckering of aspen. This creates extremely unfavourable conditions for spruce regeneration and an almost pure stand of aspen will develop. When intense fires destroy the humus layer, however, mineral soil is exposed and the vigor of aspen suckers reduced. Conditions conducive to white spruce invasion are thus created, assuming both a seed source and favourable weather.

Rowe (1961) stated that the structural irregularity observed in the absence of fire results from a filling-in process. It may occur rapidly when initial disturbance favours rapid invasion by white spruce and much slower when conditions favour

the establishment of aspen, balsam poplar, paper birch, or pine. In this case, the spruce slowly fill in gaps left by the other species as they die. The stand then stagnates with replacement only on favourable seedbeds (stumps and rotten logs) and balsam fir becomes increasingly abundant. In spruce-fir forests of northern Alberta highlands, balsam fir was dominant in only a few stands which occurred at higher elevations (Achuff 1974) and presumably on more mesic sites.

In a study of forest conditions on the lower Peace River, Lacate et al. (1965) concluded that following fire on xeric uplands succession proceeded much as Raup (1946) described. On mesic sites, fire left residual timber patches. These generally developed a "scrub" cover of aspen, willow, paper birch, white spruce, and balsam poplar with local patches of alder, tamarack, black spruce, or jack pine. Often it consisted of just aspen with a white spruce understory. The aspen and many of the shrubs and herbs may die out at about 100 years and are replaced by white spruce. Fire usually occurs by this time, however, restoring initial scrub conditions. If fire is absent, all the aspen and balsam poplar will die after 150 years, leaving an even-aged pure spruce stand. Decay is common past this point, and small openings are created by wind and other natural forces. White spruce may reproduce, or deciduous species, particularly aspen, may sucker in these openings giving the stand a mixedwood aspect.

Balsam poplar usually survives longer than aspen. On mesic sites in Alberta in 50 year old stands, 78% of aspen and 30% balsam poplar were infected by fungi, while in 80 year old stands, the values were 85% and 75%, respectively. In addition, balsam poplar was only 10% decayed on a volume basis while aspen was 5% decayed (Thomas et al. 1960).

Stringer (1976) only briefly discussed upland succession on the AOSERP study area. He observed that most dry sandy sites were covered with aspen or jack pine. He felt that the aspen would be invaded by white spruce, eventually developing into a

coniferous forest of white spruce and perhaps some balsam fir. However, he also stated that "the nature of fire-free forest is largely a matter of conjecture" as there are "many stands dominated by aspen, jack pine and white and black spruce beneath which there is little or no reproduction and therefore no evidence of succession". In his Upland Mixedwood and Coniferous Forest type, on the upland sandy sites, black spruce appeared to be succeeding jack pine as it was the only species reproducing successfully.

In his study of northern Alberta highland spruce-fir stands, Achuff (1974) sampled four stands near the southern edge of the AOSERP study area. He considered that the aspen and/or pine stands would outgrow white or black spruce for about 50 to 75 years for aspen and 75 to 120 years for pine, when spruce would become dominant. Balsam fir would also invade at about this time. No stands were old enough to be second generation stands, since fir can live for 200 years and white spruce over 300 years (Horton 1956). Achuff (1974) noted two sources of indirect evidence of the permanence of spruce-fir forest in the absence of fire. These were population age structures of spruce-fir forest and lack of evidence of any vegetation types being able to replace it. Achuff (1974) concluded: "There is evidence of increasing amounts of fir for the first 200 years or so, but the trend apparently does not appear to continue to pure fir forest".

It is interesting to speculate that perhaps with the differing life spans, dominance may change alternately between spruce and fir in the absence of fire. This has been noted in other areas by Watt (1947), Evans and Cain (1952) and Dansereau (1956).

4.2.4 Lowlands

Lacate et al. (1965) gave an account of succession on alluvial lowlands as follows: after fires, only residual patches of spruce and poplar remain. Commonly, aspen with a white spruce understory develops but often a scrub type of willow, balsam

poplar, aspen, paper birch, and alder is formed with a white spruce understory. If a seed source is nearby, an almost pure stand of white spruce can form. By 150 years, the balsam poplar (the longest lived of the scrub type) become decadent and alder, dogwoods, and other tall shrubs develop in less densely stocked areas. The poplars die before 200 years and the spruce thin naturally. This invites luxuriant shrub growth, mainly alder and paper birch which sprout locally. White spruce also reproduces in these natural openings.

Stringer (1976) found that balsam poplar existed in almost pure stands on favourable sites in the AOSERP study area; the trees were up to 65 cm in diameter and nearly 30 m in height. Some medium-to-large white spruce and aspen were present but regeneration was sparse or absent.

Raup (1946) felt that Flood Plain White Spruce forest of the Athabasca-Slave Lake areas developed from shore line or wet meadow sites. It could follow two basic pathways. On local sandbars, the sequence was *Salix interior*, occasionally with *S. lasiandra*, *S. lutea*, and *S. bebbiana*. This was followed by alder and balsam poplar which would then develop into a white spruce type. Slough areas usually followed a *Salix planifolia*, *S. petiolaris*, and *S. bebbiana* sequence. Their successional sequences then are similar to those along meandering rivers.

Small scattered grasslands grow on drier sites on lowlands. Lewis (1977) cited several authors and interviewees who indicated that Indians maintained grasslands with fire and burned forests on sites favourable to grassland species. Since settlement, most of these have reverted to forests; hence, grasslands are less extensive than in the past. On the Peace River, grasslands may sometimes be reproduced in the succession sequence, but they are eventually invaded by aspen and willow (Jeffrey 1961). Invasion by trees may have been prevented by fires set on purpose in pre-settlement times.

4.2.5 Understory

The trend of succession on most mesic and wet sites in the boreal forest is from deciduous to coniferous and from open to closed stands. The understory similarly undergoes at least as drastic a change as the overstory (Figure 21).

Rowe (1956) described the relationship of canopy to understory as: "The principal factor controlling the structure of the undergrowth is light, for although temperature, root competition, litter accumulation, and other soil characteristics exert a subsidiary effect, their main influence is on composition rather than stratification". The canopy or any layer that allows substantial amounts of light to penetrate permits the layer below it to flourish. In general, the relative height of forest species at maturity is inversely related to their shade tolerance (Rowe 1956).

The understory in aspen-dominated stands of the mixedwood section of Alberta consists of the following (La Roi 1967b). The medium shrub layer contains *Cornus stolonifera, Rubus strigosus,* and *Viburnum edule* on mesic sites; *Rosa acicularis, Ribes triste, Lonicera involucrata,* and *Symphoricarpus albus* on more xeric sites. In or below this stratum, the herbaceous vegetation includes *Aralia nudicaulis, Mertensia paniculata, Aster* spp. *Lathyrus ochroleucus, Vicia americana, Calamagrostis canadensis* and, in dry openings, *Calamagrostis rubescens.* The dwarf shrub-low herb stratum contains *Linnaea borealis, Fragaria* spp., *Cornus canadensis, Mitella nuda, Equisetum* spp., *Rubus pubescens* or *R. acaulis,* and *Pyrola* spp.

In spruce-dominated mixedwood forest, the shrub layer is usually represented by *Alnus crispa, Viburnum edule,* and *Rosa acicularis*; the latter two are also found in aspen-dominated stands (La Roi 1967b). In the dwarf shrub-low herb layer, *Cornus canadensis, Linnaea borealis, Equisetum* spp., *Pyrola* spp., and *Mitella nuda* appear to be carry-overs from the aspen-dominated stage. *Vaccinium vitis-idaea* and *Comandra* spp. represent new additions but *Fragaria* spp. and *Rubus* spp. are eliminated. In

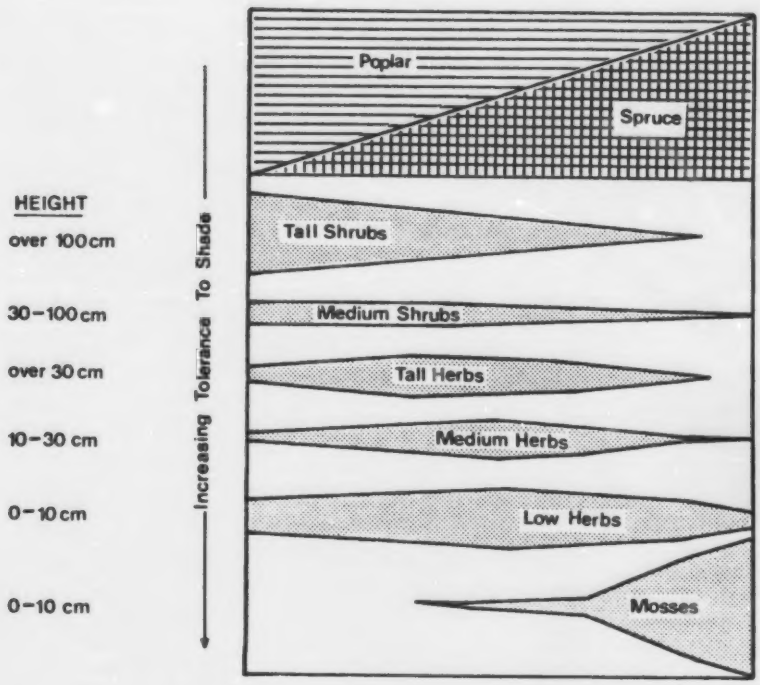

Figure 21. The relative cover-abundance of undergrowth strata in mature stands of poplar, poplar-spruce, and spruce. Data from quadrat studies in 20 representative stands (modified from Rowe 1956).

addition, feather mosses (*Hylocomium splendens, Pleurozium schreberi, Ptilium crista-castrensis*) dominate the surface. Also noteworthy is the apparent lack of a tall herbaceous stratum. This is probably attributable to these species being shade intolerant. The carry-over of dwarf shrub-low herb species is probably attributable to their shade tolerance. These observations lend support to the inverse relationship between height and shade tolerance.

Rowe (1956) examined the relationships between stratal position and site moisture for understory species of the mixedwoods of Saskatchewan and Manitoba. For moist, very moist, and wet types, lower strata increased and the shade intolerant taller layers decreased as the tree canopy closed, although species composition changed. On the dry and very dry sites, light was apparently not limiting as these stands are generally more open; no comparisons of statal dominance were made. On fresh sites in the more open pine, poplar, spruce, or mixed forests, the tall and medium herb layers included *Aralia nudicaulis, Epilobium angustifolium, Actaea rubra, Aster ciliolatus, Disporum trachycarpum*, and *Viola rugulosa*. Under closed tree canopies, the medium and low herbaceous layer included *Oryzopsis asperifolia, Galium septentrionale, Maianthemum canadensis*, and *Pyrola* spp. There were similar changes in the understory structure for moist, very moist, and wet forest types.

In the moist forest, feather moss was rarely present until the stands were 70 or more years of age, but they were present in young stands of the very moist forest. Rowe (1956) stated that the delay in invasion by mosses was due to almost daily desiccation by direct sunlight and smothering by the sudden release of the broad, flat leaves of deciduous trees. In contrast, the shaded, moister conditions under coniferous canopies encouraged the growth and gradual release of the small thin needles which do not smother the mosses. Figure 21 shows the change of relative cover abundance values for the various

strata as the relative composition of aspen and spruce overstory changes.

Considerable change also takes place at the soil surface. In aspen or other deciduous stands, the amount of light reaching the surface is much greater, particularly before leaf set and after leaf fall. This results in a warmer habitat which encourages rapid growth of early spring plants and the decomposition of fallen leaves. Because of the lack of a moss carpet, soil temperatures may often be higher than under spruce. Litter of deciduous origin is much more readily decomposed by a number of invertebrates, bacteria, and other decomposers due to a higher soil pH, less resistant material, higher temperatures, and the ease with which precipitation reaches and penetrates the surface mulch. The active mixing at the soil surface by invertebrates and vertebrates, as well as the rapid decomposition to readily usable forms, permits rapid recycling of nutrients and provides an almost ideal seedbed for many plants.

In coniferous stands, however, the opposite is generally true. Temperatures are relatively cold due to the intense shading. The needles are decomposed mainly by fungi at the lower soil pH and chemically are more difficult to utilize. In addition, the moss carpet intercepts precipitation that was not intercepted by the heavy spruce canopy. Showers and light rains may never reach the soil surface. When sufficient precipitation or snowmelt does penetrate the coniferous mulch, it picks up organic acids which promote leaching of nutrients. More nutrients are also bound in the accumulation of organic matter that builds up due to slow decomposition. As a result, the combination of low temperatures, poor nutrient status, and low light levels creates conditions where only a few species can germinate and become established.

5. CLASSIFICATION OF VEGETATION

There are no clear, standard definitions of what communities are or how they develop; descriptions of scientific observations are often coloured by the author's interpretation of communities and succession. Consequently, a summary of ecological thinking as it developed in North America is included to illustrate the various thoughts running through the scientific literature.

5.1 COMMUNITIES, CLIMAX, AND SUCCESSION - A BRIEF REVIEW

The concepts of communities, climax, and succession have been the subject of extensive debate over the years. Some investigators have strongly adhered to the idea of orderly replacement of plant communities until a self-perpetuating community develops, regardless of initial conditions. Others have critized this view, claiming it ignores the variability of plant species and the diversity of stands observed under what appeared to be similar conditions. Instead, they believe that plant communities do not exist and view vegetation simply as an assemblage of species brought together by chance and the interaction of the species' tolerances, and a site's initial conditions, environment, and history. Other investigators have taken intermediate positions, acknowledging the extreme views and adapting each as appropriate to a particular study.

Throughout this report, the term "climax" has been avoided because its dogmatic connotation greatly reduces its usefulness. The term "succession" is used to imply observed change through time without implying a predetermined reference or end point. "Community" is used to describe assemblages of species.

Diverse views on the nature, dynamics, development, stability, and continued existence of a plant community are not surprising, considering the complexity and diversity of plant form, structure, and interactions displayed over diverse landscapes, and considering the history and evolution of plant ecology

concepts around the world. The only element common to most definitions of "community" seems to be "a group of populations which occur together". It is usually applied to an assemblage of populations which are readily recognized, spatially delimited, and contain a dominant descriptive biological or physical attribute. Examples include the oak-hickory forest, black spruce-bog, tall grass prairie, or floodplain forest.

Communities can also be defined by functional relationships rather than descriptions. A functional definition such as "a population of interacting organisms" implies spatial continuity but does not demand it. Regardless of how or where boundaries are arbitrarily set, there will be interactions with other similar units. It may be best to delimit communities as assemblages of populations that interact more with each other than with adjacent assemblages. This concept of community will remain useful as long as the criteria used for delimiting the community are explicity defined and understood.

The perception of how vegetation develops is closely related to the perception of what a community is. North American and English ecologists were strongly influenced by the dynamic view of vegetation of Clements (1916, 1928) who observed constant changes in the undisturbed or recently disturbed vegetation in North America. Clements likened the formation to an organism, an entity which was more than a sum of its parts. This was given added creditability by Smuts (1926) whose "holist" philosophy viewed the universe in a like manner. Clement's fundamental unit was the plant formation, the "proper" regional vegetation, and a climatic climax for each climatic region. Viewed as a complex organism, this formation could arise, grow, mature, and die. The climax formation would inevitably develop on newly-exposed or disturbed sites. Each seral community was believed to create conditions more favorable for the next stage and less so for itself. This was viewed as a continual, directional, and predictable process moving toward a self-perpetuating, mature climax

community in equilibrium with its environment. Clements felt that this climax was determined by climate. This is the classical view of succession.

Tansley (1920) disagreed with the concept of a single climax for an area. His polyclimax theory considered the climax to be controlled by local site factors, since sand dunes and peat bogs, for example, were unlikely to develop the same community under the same climate. Tansley did feel, however, that the community behaved as an entity in many respects. The analogy between vegetation and organisms eventually led him to the ecosystem concept (Tansley 1935).

In contrast to these "organism" views of vegetation, H.A. Gleason (1917, 1926) considered vegetation to be unique at any point in time and space. Communities were not an organic entity or holistic in nature. They were merely the coincidence of species interacting with their environment. Since site conditions and environments change constantly, and since no two species have the same requirements, Gleason concluded that no two areas could be considered as closely related. This is his "individualistic" concept of plant communities.

These ideas were initially rejected and dismissed; but by the late 1940's, they were revived and adapted by the Wisconsin school of plant ecology with its "continuum" view of vegetation. This view denies the existence of community boundaries since species vary in importance along environmental gradients. Proponents argued that if communities are entities there should be points in space with little overlap of species importance, but Curtis and McIntosh (1951), Curtis (1955, 1959), Whittaker (1956, 1967), and others found extensive overlaps. Discontinuities, however, have been noted by numerous other ecologists (Dahl 1957; Daubenmire 1968, Stephenson and Stephenson 1961, Egler 1968), who claim, in part, that the lack of discontinuities is an inevitable consequence of data analysis techniques used.

The recent "climax-pattern hypothesis" (Whittaker 1953, 1962, 1970; Selleck 1960) incorporates some aspects of the traditional succession/climax and the continuum view. The "climax pattern hypothesis" professes that composition, species structure, and functional balance are determined by the total environment of the ecosystem, not by one or even a few aspects. In addition to general habitat characteristics, the availability of flora and fauna and their chance dispersal are important aspects. As the environment changes, so does vegetation. The overall result is a mosaic of climax types; the central and most widespread is deemed the "prevailing climax".

Horn (1975) postulated that the composition of community mosaics in a many specied forest depended on probabilities of success among competing species during the colonization and replacement stages. Probabilities of successive generations eventually reach a stationary state, in which the proportion of canopy species remains constant in the absence of disturbance. He defined this stationary state as the climax of an area.

Watt (1947), Evans and Cain (1952), Dansereau (1956), and others proposed that climax or mature communities may alternate on the same site through time. This idea is similar to succession except that the end point consists of two or more alternating types rather than a single community.

In recent years, the ecosystem has replaced the plant community (society, formation, or association) as the central ecological unit. As a result, succession is usually seen to lead to stable ecosystems rather than only stable vegetative units. This has considerably increased the complexity of the problem but has led to a number of new approaches to help explain succession.

Odum (1971) listed 24 trends of ecological succession under six general headings: community, energetics, community structure, life histories, nutrient cycling, selection pressure, and overall homeostasis. Although these have been criticized by Peters (1976) as being tautological in part and some being in error

(Drury and Nisbet 1973), they form a core of ideas around which investigations on the nature, structure, and function of ecosystems have focussed in recent years. Their limitations as theories must be firmly kept in mind since they are not applicable to all sites or conditions.

Community energetics in most terrestrial ecosystems appear to be characterized by initially high gross productivity-to-respiration ratios which approach unity as maturity is approached. This implies that biomass is being added until maturity when energy fixed approximates that needed for maintenance. Gross and net community productivity per unit of standing crop would thus progress from high to low. Conversely, the amount of biomass supported per unit of energy flow is initially low and continually increases as maturity approaches. Food chains become more complex and weblike as more biomass (and diversity) is added and the decomposer component increases relative to the consumer component. Exceptions to these general trends exist; Drury and Nisbet (1973) reported on studies where increased diversity produced no demonstrated increase in productivity.

Community structure is intertwined with community energetics. Since total organic biomass in mature ecosystems is initially lower, a large portion of nutrients is biologically unbound and species and the biochemical diversity develop. The additional time and complexity changes the "texture" from relatively poor spatial definition to a well-organized unit.

During maturation, nutrient cycling changes to a more closed system; exchange rates between the biotic and abiotic portion of the ecosystem decrease, and the detritus component increases in importance.

Selection processes initially favor species which are adapted to rapid colonization and those with high rates of reproduction and growth (r-selected species). They, in turn, are replaced by K-selected species that are adapted to more permanent, competitive situations. This is believed to result from increased species and numbers (Cody 1966; MacArthur and Wilson 1967).

Initially, communities are considered to be characterized by those organisms with less niche specialization, with simpler life cycles, and of generally smaller size than most mature community occupants. Drury and Nisbet (1973), however, pointed out that many plant species of the mature community are often present from the beginning.

Within the mature community, overall homeostasis is generally considered to be higher because of internal symbiosis, nutrient conservation, higher resistance to external perturbation, and lower entropy (higher "information" content). Drury and Nisbet (1973) and Colinvaux (1973) noted that this view on stability is not always borne out by observation.

The concepts of communities, climax, and succession are currently undergoing extensive discussion and review. These are being revised and adapted as new data arise, but comprehensive theories are lacking. In reviewing and interpreting literature dealing with the ecology of vegetation, such as that found on the AOSERP study area, one must, therefore, keep in mind previous concepts and views held by the authors since they affect interpretation of the data.

5.2 CLASSIFYING VEGETATION

Classification, the grouping of what are believed to be related phenomena because they are judged to be "similar", is a fundamental characteristic of man. Things must be grouped to allow one to deal with masses of facts. Indeed, Egler (1977) considered classification to be a psychological necessity. Beginning in the 1800's, ecologists, faced with ever increasing information about new plant communities in different parts of the world, began to develop systems of grouping these data.

The goal of any classification system is to group units related by the greatest number of "significant" characteristics. It must be based on those characteristics that serve as indicators of the greatest number of other "important" aspects. Thus, talking

about one group and its characteristics allows one to portray a great deal of additional related information about the group. The difficulty arises in deciding what is "significant" or "important".

What is judged to be "significant" or "important" has varied with the individual investigator, his heritage, his knowledge, his experience, his biases, the vegetation he knew, and the purpose of the classification. Some investigators judged appearance and physiognomy as most important and classified on this basis. Others observed that such systems dealt inadequately with species composition and, believing it to be of greater importance, proposed classifications based on floristics. Yet others were impressed by environmental or successional relationships and proposed classification using these criteria. The result has been a proliferation of proposed vegetation classifications, to the point of "as many opinions as there are men" (Shimwell 1972).

All classification systems are artificial. No system is inherently correct for all areas and problems, and the existence of one system does not invalidate the others. Many systems are not directly comparable, since they establish incommensurable groups. Although a complete description of a landscape is impossible, there should be enough well-defined units to include most of the significant stand variation. Ultimately, the selection of a classification system must be based on the problems to be addressed, study objectives, and the use of the results. Whittaker (1962) concluded: "The classification must be viewed as a cultural product, understood in a context which includes both cultural values and ecological conditions, and judged in its functional relation to present understanding and practice".

This section briefly describes the history, methods, and uses of the following five major approaches to studying and classifying vegetation: (1) physiognomic classifications; (2) the ordination (continuum) view of vegetation; (3) formal floristic classifications; (4) the North American approach of informal classification based on dominance and physiognomy; and (5) biophysical land classifications.

5.2.1 Physiognomic Classification

Physiognomic classifications are based on form (appearance) and structure (arrangement in space) of the vegetation components. Such systems are relatively simple and the easiest to understand or "believe in" (Egler 1977), since they include such familiar terms as "forest", "desert", or "meadow". Egler (1977) believes them "to have been based on valid working hypotheses, for their times", indicating that such systems are no longer sufficient by themselves.

Whittaker (1962) traced the early history and development of these types of classifications. Shimwell (1972) expanded on this and described the various related systems which are based on physiognomic characteristics of form, function, and structure. Such systems are relatively easy to understand and use because, to a certain extent, physiognomically similar communities (formations) occur on parts of different continents with similar environmental conditions (Whittaker 1962). These correspondences were a major justification for the physiognomic approach to vegetation. They allow grouping into a world-wide hierarchical classification.

Many physiognomic classifications have been proposed. Two have recently been developed and used (Fosberg 1967; Mueller-Dombois and Ellenberg 1974). Fosberg's system was proposed (Peterken 1967) and used during the International Biological Programme inventory of possible sites for designation as ecological reserves in Canada (e.g., La Roi et al. 1976).

Fosberg (1967:74) designed his physiognomic classification to have the following features in order for it to be most useful:

> "(1) It must be possible to apply it even with the minimum of information commonly available. (2) It must be applicable to all macroscopic vegetation, or at least be capable of expansion to accommodate all types that cover mappable areas at ordinary scales. (3) It must convey or be adaptable to convey the kinds of information useful to a wide range of users of vegetation data. (4) It must be capable of refinement to utilize and convey

> detailed and quantitative information when this is available. (5) Its terminology must, in itself, convey a substantial amount of information about the vegetation. (6) It must be based entirely on the features of the plants themselves, without involving features of the physical or animal environment."

He subdivided vegetation into successively smaller units to the lowest level at which vegetation structure and function provide a clear separation of units. Finer subdivisions must be based on floristic criteria, either associations in the sense of Braun-Blanquet (see Floristic Classification) or by dominant species (see Informal Classification by Dominance and Physiognomy).

The primary division is based on the spacing of visible portions of the vegetation. Three primary structural groups result--closed, open, and sparse. At the next level, habit and stature are used as criteria to determine whether the formation class is forest, scrub, grass, savanna, meadow, or steppe. Below this level, the formation group is determined by whether the dominant layer is evergreen, deciduous, or otherwise seasonally dormant. The smallest subdivision in this system, the formation, is based on the dominant growth form with emphasis on leaf texture.

Since the system is so simple, few data per se are needed to classify any vegetation, at least to the level of formation class or group. Only recent air photos are needed for broad classification, mapping, or selection of stands warranting detailed floristic and environmental study. At this stage, familiarity with the vegetation becomes more important.

The system offers numerous advantages. It is a practical tool for mapping vegetation and organizing data for general purposes (Mueller-Dombois and Ellenberg 1974). It is particularly useful for reconnaissance vegetation surveys since it can be applied to air photos, is based on existing stable vegetation, provides a general picture capable of later refinement (Reid 1974), and can be used to help select sites for detailed floristic and environmental sampling. Floristic relationships within and

between units can be determined, and structural vegetation patterns can be compared to climate, soil, history, and other environmental maps to help derive major regional or zonal ecosystems (Mueller-Dombois and Ellenberg 1974).

The ease and simplicity of the system are also its disadvantages. The resulting classification is broad and of itself says nothing about the floristic composition--but this can be overcome by appropriate detailed studies. These studies, however, can reveal that floristically related types are separated because their spacing, form, or structure differs; or they can show that ecologically quite different types are grouped into the same unit (Mueller-Dombois and Ellenberg 1974).

The Fosberg (1967) physiognomic classification has been used in the International Biological Programme Conservation of Terrestrial Ecosystems in Canada (La Roi et al. 1976). Of more direct relevance to AOSERP, the system has also been used in the reconnnaissance vegetation surveys associated with the Mackenzie Valley gas pipeline proposal (Hettinger et al. 1973; Reid 1974; Reid and Janz 1974; Hettinger and Janz 1974; Reid and Calder 1977). Many of these studies were in areas close to, or having vegetation similar to that, in the AOSERP study area. Air photo interpretation was supplemented by detailed site sampling to characterize vegetation units (on the basis of layer dominants) within the formation classes identified. Viereck (1975) similarly used Fosberg's (1967) system to classify Alaska taiga vegetation and, where appropriate, used Reid's (1974) vegetation units within the formation classes.

5.2.2 Ordination and the Continuum Concept

The ordination approach arose from the concept that vegetation exists as a continuum, not as discrete "natural" units. It involves a fundamental difference in how one views vegetation and is not simply a disagreement on methodology.

Ordination, strictly speaking, is not a system of classifying vegetation although its mathematical techniques have been used to organize and interpret data from sampled sites. These

techniques, themselves, are now used in a wide variety of vegetation studies including traditional and formal classification schemes. Though disagreeing fundamentally with the philosophic concept of vegetation as a continuum, they accept ordination techniques as useful tools for data analysis.

Whittaker (1962) and McIntosh (1967) traced the history of this "individualistic dissent" in the various regions of Europe and North America since the 1920's. Gleason (1926, 1939), in his "individualistic concept of the plant association", concluded that an association is merely a coincidence resulting from environmental sorting of plant populations. His ideas and those of European authors were quickly rejected, ridiculed, or dismissed as unworthy of serious consideration (Whittaker 1962; McIntosh 1967). By the late 1940's, however, these concepts resurfaced in North America, particularly in the studies of Curtis (1959) and his students in Wisconsin. Since then, they have been extensively discussed and debated [(e.g., see review by McIntosh (1967) and comments on it in Dansereau (1968); Whittaker (1962, 1967); chapters in Mueller-Dombois and Ellenberg (1974); Shimwell (1972)].

Supporters of the continuum concept recognize units of vegetation and "classify" their samples, but only as required for discussion and only to help data analysis and interpretation. Vegetation is seen as a complex and largely continuous population- "a gradient of communities in which species are distributed in a continuously shifting series of combinations and proportions in a definite sequence or pattern. It is clear that these are not random combinations of species nor are they unrelated to the environment" (McIntosh 1967). They do not accept, however, that vegetation exists in nature as the discrete units obtained by classification.

Critics of the continuum concept [(e.g., Daubenmire 1966; discussions in McIntosh (1967) and Dansereau (1968)] attacked the results and findings of ordination studies and gradient analysis as being artifacts or inevitable consequences of the data sampling and handling methods used (e.g., Egler 1968; Daubenmire 1966). Many

other authors (e.g., Shimwell 1972; Anderson 1965; Whittaker 1962; McIntosh 1967, 1968; Goodall 1970) pointed out that the controversy is largely semantic and a difference of viewpoint. Neither approach is "correct"; both are different ways of looking at vegetation. Whether a particular problem is investigated by a classification or a continuum approach will depend largely on the terms of reference of the investigator, his background, knowledge, and biases. Techniques developed during ordination studies have been adapted and used in formal classification studies, including those of the Zurich-Montpelier school [e.g., see Maarel 1969; examples in Shimwell (1972) and Mueller-Dombois and Ellenberg (1974)].

Ordination methodologies have evolved since the early 1950's (Curtis and McIntosh 1951) when one-dimensional ordinations or linear arrangements of index values for sampled stands were used. A multi-dimensional technique was developed by Bray and Curtis (1957) which, with modifications and adaptations (Beals 1960, Swan and Dix 1966), has been adapted and is now used extensively and routinely in numerous vegetation studies. This multi-dimensional methodology has been detailed with examples in Mueller-Dombois and Ellenberg (1974) and Shimwell (1972). Using this method, stand similarities are used as a basis of determining their relative positions along multi-dimensional (usually two or three) axes also determined from stand data.

Ordination usually requires some quantitative stand data, although Goodall (1970) pointed out that presence/absence species data may be used in suitable sized quadrats. The most common quantitative measure now used in North American studies is the species prominence value (P.V.), where P.V. = (mean cover or cover class mid-point percent) x (square root of frequency). This requires sampling several quadrats per stand and estimating cover, usually using a cover-class scale. Frequency is determined by the proportion of quadrats per stand in which the species is present.

The following advantages of ordination refer to the mathematical treatment of stand data, not to the philosophic aspects of whether vegetation is continuous or composed of discrete units. Ordination allows graphical portrayal of the

relative positions of a set of sampled stands. The method is useful for plotting or visualizing relationships, and environmental data can be superimposed on the resulting graphs to help determine correlations between stand relationships and environment.

Two- or three-dimensional ordinations, however, may distort stand relationships because the distance measure used to determine relative positions is not a true Euclidean distance. Since negative distances can arise, two stands may be shown as having zero distances even though they are not identical. The sum of two sides of a triangle formed by three stands may also be less than the third side, suggesting that the sides are not straight lines (Shimwell 1972). This may indicate a need for additional axes. Visualization in Euclidean hyperspace, however, is impossible and can lead to confusion for those without a reasonably strong mathematical background.

Ordination methods have been extensively used since their introduction by Bray and Curtis (1957). McIntosh (1967), Whittaker (1962, 1967), and their supporters and followers have used the results to support their concept of vegetation as a continuum. Equally, however, the techniques have been used to assist in formal classifications of vegetation. Mueller-Dombois and Ellenberg (1974) considered it to be the step prior to classification, and Maarel (1969) has used it to classify stands using floristic similarity. Ordination is only one way of helping interpret stand data; it should not be considered as being the one "correct" way to classify or analyse plant communities.

Ordination studies have been carried out in boreal forest areas at Candle Lake, Saskatchewan, east of the AOSERP study area (Swan and Dix 1966; Jeglum et al. 1971). Douglas (1974) also ordinated his montane zone vegetation in the southwestern Yukon.

5.2.3 Floristic Classification

Classifications of vegetation based solely on floristic composition and distribution arose largely in Europe after the

turn of the century. These systems have been developed most extensively there, particularly as a result of Braun-Blanquet (1932) and his followers. Over the decades, the many European schools of thought on vegetation classification have debated their differing approaches and concepts. Since the 1950's, however, agreement has generally been reached on terminology and a hierarchical nomenclature. Although differences in concepts may still arise, there is an agreed-to methodology for sampling, describing, and classifying vegetation. The history, evolution, and discussions which led to the present situation have been thoroughly detailed by Whittaker (1962), Becking (1957), Shimwell (1972), Mueller-Dombois and Ellenberg (1974), and, to a lesser extent, McIntosh (1967).

This section focuses on the current approach and methods used by the dominant European school, the so-called Zurich-Montpellier (Z-M) or Braun-Blanquet school. In addition, the concepts and approaches originally developed in Scandinavia and how they now fit into the dominant Z-M system are examined since the vegetation where they were developed is similar to that in the AOSERP study area and since they contributed so much to North American ecological thinking.

5.2.3.1 Description of the Z-M System of Classification. Central to the Z-M school of classification is the belief that vegetation exists as discrete, classifiable units called associations. The system has developed detailed rules and methods on sampling, detecting, naming, and classifying these associations on the basis of their floristic composition. The chief criterion for separating associations is character species, those species with distribution generally restricted to one association. This contrasts with the approach in North America, and originally in Scandinavia, where dominant species were used.

Until recently, there were few English descriptions of the system, apart from a translation of the pioneering work by

Braun-Blanquet (1932). Most studies and concepts were developed and described in German and French. Beginning in the mid-1950's, however, evaluation and explanations of the system began to be published in English (e.g., Poore 1955a, 1955b, 1956; Becking 1957; Moore 1962; Whittaker 1962). Recently, Shimwell (1972), and especially Mueller-Dombois and Ellenberg (1974), have given detailed step-by-step descriptions of the methods involved. These are briefly summarized below but the above references, particularly the last two, should be consulted for details.

Application of the system requires extensive collection of representative stand samples. Stands must be uniform, representative of the vegetation types in the area, undisturbed, and of at least the minimum area for that type of vegetation (at least 200 m^2 for forests, but only 10 m^2 for grasslands). Sample choice is thus quite subjective. The minimum area must be sampled in each stand. Once a stand is selected, sampling is straightforward. It consists of the standard notations about the site (location, slope, aspect, elevation) and its general characteristics (layering and percent cover for each, soil type and horizons, root layering distribution). All vascular and cryptogamic species present are listed; for each, two numerical ratings are noted. One is a scale which combines cover and abundance (5 = cover more than 75% of the area; 4 = cover 50 to 75%; 3 = cover 25 to 50%; 2 = cover 5 to 25%; 1 = numerous individuals but total cover less than 5%; + = few individuals with little total cover; r = solitary and little total cover). The other scale indicates the sociability of each species--how it is distributed in the stand (5 = growing in large, almost pure populations; 4 = growing in small colonies or forming large carpets; 3 = forming small patches or cushions; 2 = forming clumps or dense groups; 1 = growing solitarily).

When a representative number of stands have been sampled, all stand data are aggregated on one raw table. The table is examined to identify mutually associated species which may help differentiate groups of stands. This step is the most controversial

aspect of the method and has been likened more as an acquired art than a science. Moore (1962) agrees that it is "a craft to which one must be apprenticed". Mueller-Dombois and Ellenberg (1974), and to a lesser extent Shimwell (1972), have described the step-by-step procedures in this process, removing as much subjectivity as possible in the identification of character species based on their constancy in the grouped stands. These groups are compared with already published descriptions to see if they belong to previously identified associations, as defined by their character species; if not, a new association is described. Detailed rules exist for naming associations and classifying them into higher units called alliances, orders, and classes, again on the basis of diagnostic species. Recently, computerized methods have been developed which help identify species groups in stand data (Moore et al. 1970; Ceska and Roemer 1971). In many cases, these higher units correspond to vegetation types or units recognized by those working outside the system. These higher units also often appear most useful in relation to environmental factors, physiognomy, and dominant species (Whittaker 1962).

Mueller-Dombois and Ellenberg (1974) and Shimwell (1972) described how the concepts of association, alliance, and order have evolved as more and more areas of Europe were described by the Z-M method. These changes resulted from a narrowing of the assocation concept, as well as a greater knowledge of species distribution over a wider area.

Actual data needs for applying the Z-M system are minimal. What is needed, however, is a knowledge of and familiarity with the concepts and methods used in identifying associations by followers of the system. A thorough familiarity with the flora and their distribution is a basic necessity. These aspects can be learned and require practice (e.g., in selecting "typical" and "uniform" sites) but the skills needed are ultimately no more stringent than those needed for any effective study of vegetation.

Whittaker (1962) has discussed the advantages and disadvantages of the Z-M system and concluded (p.139) "considered, with its limitations clarified and accepted, the system is the most successful and most widely applicable means of formal classification that has yet developed". He presented the following as advantages:

To those familiar with the system and the vegetation, hierarchical classifications portray a great deal of information on species relations, communities, and habitat relations in a concise way that cannot be matched by other classifications.

The use of diagnostic species on all levels of this system gives a coherence and consistency lacking in others and has proved successful for vegetation classification in virtually all areas of the world.

The standardization of concepts and methods is an advantage that allows integration of numerous studies into a master scheme, and allows the work of one author to be interpreted directly and used by others. The standardization of methods tends to require careful work since knowledge of the flora is necessary, detailed stand records must be compiled to allow community description and classification, and definition of associations must be specific and based on designated diagnostic species.

Some of the major developments in intensive ecological application have come from this school and not from other systems.

Two of the disadvantages of the system are of a practical nature. One must be thoroughly familiar with the system and its concepts as well as with the flora of the study area. In addition, only one large plot is sampled per stand in contrast to the North American tradition of numerous smaller plots.

Many of the other disadvantages and criticisms of the Z-M system have been philosophic. These were discussed by Whittaker (1962). Criticisms that the system is extremely subjective have little validity since it is inherently no more subjective than any other system of classification.

Although adherents of the system claim character species are objectively selected and used as the only criterion to delimit associations, it seems clear that dominance and habitat are used in practice to group stand data and help identify associations which are secondarily rationalized by specifying character species.

The major criticism of the system (related to the above) has been directed towards the doctrinaire formalism of the school and its insistence that it is the way of studying vegetation. The system is effective and highly successful but criticism of its concepts has often resulted in avoidance reactions rather than consideration of the merits of the criticism. The strongly formal aspects of the system may lead to routine and doctrinaire acceptance of the system and classification of vegetation for its own sake rather than as a tool to investigate ecological questions.

Regarding the proposal that the Z-M system be adopted as the standard method of studying vegetation, Whittaker (1962:140) concluded:

> "If the premise is accepted that there should be an internationally standardized approach to community classification, there may be little point in selecting some limitations of this system as a basis of opposition when more serious limitations affect other systems. One may, however, oppose such standardization on different grounds: (1) No underlying basis for the system exists, such as the principal of common descent and the existence of some clearly-defined or "good" species in taxonomy. (2) All approaches to ecosystems have a partial and imperfect character, and different approaches may complement one another in the study of different ecological problems. (3) The avenues of exploration of different approaches should consequently be kept open. Much as ecological science has been enriched by the school of Braun-Blanquet, it would surely be the poorer if other traditions, and the minority schools of the Southern Tradition, were absorbed into this school.
>
> It may well be questioned whether ecologists should expend, and divert in part from other desirable research, the immense amount of time required to establish a classification of this type for North America. On the other hand, it would surely be of great interest to have classifications of the vegetation of some areas by this

> method, to compare with other classifications by ecologists. For intensive, detailed work in applied ecology especially, the floristic approach and concepts of diagnostic species may prove valuable, along with quantitative methods. One may thus, without advocating universal standardization of this system, suggest that its merits and achievements justify new and favorable examination by ecologists."

In North America, La Roi (1967a) carried out a study of the boreal spruce-fir forests and applied some of the Z-M sampling methodology, following stand selection based on dominance types. He used floristic criteria to arrive at a preliminary classification of the stands, but did not apply the strict nomenclatural Z-M approach for naming associations.

Application of the complete Z-M system of vegetation classification in North America, however, has been applied in the studies of V.J. Krajina and his students at the University of British Columbia. Although their methods involve use of a 10-point scale for cover-abundance and sociability ratings (in contrast to the 5-point scale of Braun-Blanquet), their site selection and hierarchical methods for naming and classifying associations are the same (e.g., see Hoefs et al. 1975).

5.2.3.2 The Scandinavian Approach. At the time that the Z-M system was being developed in central and southern Europe, different approaches arose in Scandinavia on how vegetation was to be viewed and studied. In later years, the Scandinavian and Z-M approaches merged but the original ideas of Scandinavia influenced North American ecology to a greater extent than did the Z-M system. This history and evolution has been detailed by Whittaker (1962), Shimwell (1972), and Becking (1957).

The different approaches arose largely because of the differences in vegetation. Scandinavian areas were largely poor in species and the species often occurred in large uniform patches. As a result, studies emphasized the presence of dominant species and focussed on the different layers. The concept of the association was much smaller than that of the Z-M school (it came to be

called a "sociation"). Each layer was sampled with several small quadrats. Differences between the Scandinavian approach and the Z-M school included the use of dominants rather than character species, emphasis on stratal structure and physiognomy rather than on floristic composition only, use of several quadrats, and grouping of associations by topographic and dynamic relations into vegetation complexes and by physiognomy into formations rather than by a floristic hierarchy. In recent years, those differences have been resolved through the incorporation of the sociation concept into the Z-M system as an acceptable subunit of the Z-M association and through the adoption of Z-M techniques for defining associations.

Whittaker (1962:38) concluded that, overall, the initial concepts of the Scandinavian system contributed more to North American ecological thinking than did the Z-M approach:

> "Although no one of the northern approaches has been so much used as Braun-Blanquet's, the combined influence of these northern schools on the development of ecology and phytosociology throughout the world may be even greater than that of the southern schools. The ecology of the English-speaking countries has been much more influenced by the northern schools than by Zurich-Montpellier--in the great influence of Warming and the use of dominance-types and formations, the use of Raunkiaer's life-forms and of quantitative methods from the schools of Raunkiaer and of Uppsala, and the application by individual authors of site-types, unions, and sociations. And, while the sociation has had very little use among ecologists, it became the major vegetation unit of Russian phytocenology. The magnitude of the contribution of the smaller nations of the Scandinavian and Baltic area (and of Switzerland) is one of the striking features of the history of ecology as a whole."

5.2.4 Informal Classification by Dominance and Physiognomy

North American (and other English-speaking) studies of vegetation have largely avoided formally designated hierarchical rules for classifying vegetation. The major exception was the successional system of Clements (1928) which is no longer used.

Instead, most studies have followed an informal system of classification where units are identified on the basis of dominant species as needed. As a result, the focus of these studies has been on the development of quantitative approaches for sampling natural communities and handling these data (e.g., see Goodall 1970). Whittaker (1962) and Shimwell (1972) have reviewed and traced the history and development of the North American and British approaches to studying vegetation. The following is largely based on Whittaker (1962).

North American studies of vegetation and identification of vegetation units have been relatively crude and superficial in comparison to the Z-M approach. Most subdivisions are based on the dominant species present, following initial definition of major units based on physiognomy. Such classifications may be determined by the ecologist's judgment in a context that includes vegetation characteristics, environmental conditions, and ecological purposes. As a result, units defined in the above manner do not represent a particular, standardized kind of community, and such dominance-units are poorly suited to a formal hierarchical classification.

Units can be identified on the basis of floristic composition (as in Z-M), by combination of stratal units (especially in northern vegetation), by undergrowth composition in relation to site or habitat properties, by geographic or climatic subtypes, by different combinations of dominants and subdominants, by quantitative relations (into series or complexes), or by developmental relationships into successional series.

In discussing the above informal hierarchy of vegetation units, Whittaker (1962) did not propose it as a formal system of classification comparable to the Z-M system. His objective was to offer suggestions on informal classification to be followed or disregarded as appropriate. As a result, different investigators will recognize different units, and their units may be difficult to relate to one another. He concluded (p.154):

> "Seen in comparison with the orderly hierarchy of Braun-Blanquet, this may seem a kind of chaos in classification; but if classification is not a major objective, there may be little regret that studies by different ecologists, each effective in its way, do not fit into a coherent classification. The point of the present suggestions is that if classification is not a major objective, then the experience of ecologists suggests: a physiognomic approach on higher levels, an approach through dominance-types on intermediate levels, a thoroughly fluid approach through units appropriate to circumstances on lower levels, and emphasis of environmental and dynamic relations of community-types instead of hierarchial classification."

Because of the flexibility and lack of formal rules for classifying vegetation in North American studies, no particular data need can be specified. Generally, however, the data involve an estimate of cover by species. Most studies involve the placing of several relatively small quadrats per stand (at least for understory vegetation) in comparison to the larger minimal area plots used for the Z-M method, although this approach is becoming more common. A great emphasis has been placed on random location of these quadrats within the subjectively selected, relatively homogeneous stand.

The variety of quantitative sampling techniques used is detailed in Shimwell (1972) and Mueller-Dombois and Ellenberg (1974). These include plotless techniques (point intercept, line intercept, or distance methods) as well as plot methods. A great variety of techniques has been developed for handling, organizing, and classifying the data obtained. These include ordination techniques (described previously), cluster analysis, or other statistical techniques (e.g., see Goodall 1970). Cluster analysis, in particular, has been increasingly used to help identify relationships and classify stand data.

The principal advantage of the North American approach is its flexibility. Identification of dominance types does not require thorough floristic knowledge, knowledge of the distribution of all species (on which to identify character species as needed by Z-M), extensive sampling and comparison of data before a unit can

be defined, or extensive, wide-ranging study before units can be grouped into higher categories. Little effort can be expended on classification when it is of secondary interest. Dominance-types are based on those species which seem most "important" in a community, often the species of greatest concern, particularly in applied fields such as forestry and range management.

The flexibility of the North American approach, which is its greatest advantage, is also a major disadvantage, particularly when one wants to classify vegetation and compare units from different areas.

Examples of the North American approach are numerous; they include studies by those who view vegetation as a continuum (e.g., Whittaker 1967; McIntosh 1967) as well as by those who view it as consisting of discrete communities (e.g., Daubenmire 1966). The North American approach has often been used in reconnaissance surveys of relatively large areas where extensive detailed sampling is impossible or unnecessary (e.g., La Roi 1967; Stringer 1976; Douglas 1974; Reid 1974; Reid and Janz 1974; Viereck 1975). In contrast, Hoefs et al. (1975) carried out a Z-M study and mapping of a 28 km^2 area of Sheep Mountain, Yukon, near the area where Douglas (1974) carried out his reconnaissance. This serves to point out that the objectives and use of results often determine the methodology.

5.2.5 Biophysical Land Classification

Biophysical land classifications have been proposed and developed to differentiate and classify ecologically significant segments of land surface. They are not based solely on vegetation; landform and terrain characteristics are also used. Vegetation aspects of this system have, to a great extent, followed the North American approach and sampling methods.

In Canada, biophysical classifications were developed by the National Subcommittee on Bio-physical Land Classification. The results of the committee's deliberations were published in 1969 as "Guidelines for Bio-physical Land Classification" (Lacate 1969).

The principal objective of this approach was to map and classify existing land resources relatively rapidly and provide an ecological basis for land-use planning involving future management of lands for forestry, agriculture, recreation, wildlife, and water yields. Since 1969, numerous such inventories have been carried out. The description of the system given below is largely based on Lacate (1969).

The principal aim of a biophysical land classification is to "differentiate and classify ecologically significant segments of the land surface, rapidly and at a small scale...to satisfy the need for an initial overview and inventory of forest land and associated wildland resources" (Lacate 1969). In a biophysical study, emphasis is placed on evaluating the patterns of landform, soils, vegetation, and water. Biophysical studies have two phases: a pre-field airphoto interpretation followed by field sampling selected sites, and analysis and classification of the data obtained.

There are four levels in biophysical classifications, depending on the scale of mapping. Each level is defined by different aspects of the landscape individually or in combination.

Land regions form the broadest level; mapping is at a scale of 1:1 000 000 or 1:3 000 000 or smaller. Land regions are defined on the basis of distinctive regional climate as expressed by vegetation, particularly since sufficiently detailed climatic data are lacking for many parts of Canada.

Land districts form the second level. Mapped at scales of 1:500 000 to 1:1 000 000, they are differentiated by major physiographic and/or geologic patterns. They are characterized by distinctive patterns of relief, geology, geomorphology, and associated regional vegetation.

Land systems, the third level, are generally mapped at a scale of 1:125 000. They are largely identified on the basis of landform patterns. Although soils and vegetation are heterogeneous within a land system, there is a distinctive repeated pattern associated with the landform. An example of a land system

would be: "a rolling, shallow, till plain overlying granite bedrock, characterized by Podzol soils and a yellow birch-balsam fir forest cover" (Lacate 1969:5). Land systems are one of the two working and mapping levels for biophysical studies.

Land types form the fourth and most detailed level of biophysical classification. They are usually mapped at scales of 1:10 000 to 1:20 000. They are defined as an area of land on a particular parent material, having a fairly homogeneous combination of soil (at the Soil Series level) and chronosequence of vegetation. An example of a land type would be: "a well drained portion of a gravelly outwash terrace with an Orthic Dystric Brunisol soil supporting lodgepole pine--*Vaccinium scoparium* vegetation" (Lacate 1969:6). Land types are the basic sample unit and the other principal working and mapping level.

In addition to the above system for classifying terrestrial areas, the system has a companion four-level classification for open water and wetland areas. Outlined by Adams and Zoltai (1969), it has been further developed by Zoltai et al. (1974) for wetlands. The generalized first level is based on site features involving the physiognomy of the wetland. Its main classes are bog, fen, marsh, and shallow open water. Level 2 is based on surface morphology of the wetland. Level 3 is defined on the basis of vegetation characteristics, with regional environmental influences becoming more important. Level 4, the most detailed, is subdivided and classified as needed by the particular discipline or focus of study. For example, floristic criteria are used if the study is botanical, and engineering criteria if suitability for construction is to be evaluated.

Biophysical land classifications do not have unusual data needs for the disciplines involved. The unique aspect of the system is the integration of several disciplines in one study. Within each discipline, relatively standard and common sampling methods and study approaches are generally used.

Biophysical land classification of an area requires airphotos and a multidisciplinary study team. In addition to airphoto interpretation capabilities, the study team requires knowledge of terrain, physiography, and landform identification (detailed in Lacate 1969), familiarity with soil survey methods (detailed in Agriculture Canada 1974), and knowledge of vegetation sampling methods.

Rowe (1969) outlined vegetation data needs for Lacate's (1969) biophysical classification. None is unique to a biophysical approach. Vegetation structure, along with species composition and abundance, are the major aspects studied. Vegetation should be described in physiognomically uniform plots large enough to contain the normal variety of species. Sampling should be by stratum, recording height, total cover, and species present in each layer. Species abundance is rated using a scale similar to that of Z-M. Classification of these vegetation data generally would follow the North American approach of physiognomy and dominance. Land types are often named after no more than two species but all species useful in differentiating types should be indicated. This approach resembles an informal application of Z-M principles but is basically a North American approach. The vegetation methodology used in a biophysical study, however, does not require a particular approach. Any approach appropriate to the objectives and scale of the study can be used.

The principal advantage of biophysical land classification is that it allows integration of terrain, soils, and vegetation aspects, and, possibly also, wildlife. The resulting data can be used to evaluate the suitability of an area for various land uses, including agriculture, forestry, recreation, and wildlife management. Knowledge of the vegetation supported by a disturbed area can be combined with data on soils and terrain to help develop appropriate reclamation approaches.

The use of airphoto interpretation followed by field checking of selected points allows a relatively rapid inventory of

resources, depending on the desired scale. With respect to vegetation, it has the same advantages as the North American approach.

The use of a multidisciplinary team adds to the logistical costs of the study. With a multidisciplinary study, the objectives, goals, and data needs of the study must be well thought out and the approaches developed, understood, and agreed to by all members of the study team before field sampling begins.

A preliminary biophysical classification of about half the AOSERP study area has been carried out (Thompson et al. 1978). It was based on interpretation of remote sensing data. Numerous other detailed biophysical land classifications have been carried out, many in areas of vegetation similar to those of the AOSERP study area. These include the Northern Resource Information Program for mapping northern and eastern Manitoba (e.g., Mills et al. 1976; Woo et al. 1977). Parks Canada has also carried out biophysical studies of National Parks (e.g., Gimbarzevsky 1975; Gimbarzevsky et al. 1978). Other biophysical studies include those similar to Kumar (1973) who carried out a biophysical study and capability evaluation of the Rochester map sheet of north central Alberta.

6. CONCLUSIONS AND RECOMMENDATIONS

This section discusses the conclusions and recommendations for future AOSERP vegetation studies in a general manner since it was not possible to evaluate the various development scenarios. In addition, detailed specific studies cannot be recommended now because of the as-yet-undefined nature of development. For example, although it is known that pollutants will be produced and surface vegetation destroyed, data on types of toxic substances (and especially on likely quantities) or on the extent of surface disturbance and the rate of development are not available.

6.1 VEGETATION INFORMATION NEEDS

Athabasca Oil Sands development will likely have two major categories of impact on vegetation. The first involves direct destruction of vegetation through construction of facilities and removal of overburden. The second involves indirect regional effects on vegetation, largely through modifications of drainage patterns and changes in air and water quality.

Assessing the direct impacts of facility construction and overburden removal will require knowledge, at various levels of detail, of the quantity and the quality of the vegetation affected. Development could destroy populations of rare, unique, or endangered plant species, rare or unique assemblages of plants (communities), or significant proportions of regional vegetation.

Evaluating indirect effects will require combining information on pollutants with data on the sensitivity of major plant species to identify species affected in project zones of influence. Evaluating this aspect would require knowledge of the distribution of sensitive communities and species.

6.1.1 Classification and Distribution

Information on the location and extent of existing vegetation of the AOSERP study area would provide the data base

needed to assess local and regional impacts and provide understanding of the current patterns and rates of succession.

It is unrealistic, if not impossible, to assemble a data base that contains detailed knowledge of the distribution of all plant species in the AOSERP study area. The optimum system should be able to provide information on the location and composition of communities; it should be capable of handling and integrating community and species data on a regional scale as well as on a site-specific scale; it should have the flexibility to allow refinement and calibration as new data are obtained; and it should be designed to meet overall objectives of AOSERP.

6.1.2 Succession and Ecology

Knowledge of successional aspects of vegetation in the AOSERP study area would be needed: (1) to identify pioneer species that may be of use; (2) as a standard against which reclamation can be compared; (3) to arrive at a desired end point; and (4) to evaluate indirect project effects of selective removal of sensitive species on succession.

Knowledge of pioneer species present on the AOSERP study area and their ecological site requirements and tolerances (e.g., moisture, soil type, pH, nutrient status) would help identify species that may be useful for reclamation.

Information on the general trends, rates, and patterns of succession would be required to provide a scale for evaluating the progress and success of recovery or reclamation of areas disturbed by the project, in comparison with normal recovery following natural disturbance in the AOSERP study area.

Considerable detail would be needed if the establishment of a particular end point is desired on sites disturbed by project activities. Data needed would include details on site conditions, species tolerances and requirements, and knowledge of successional pathways and conditions which lead to the desired end point. This information would be needed to create initial site conditions

suitable to the development of the desired end point, to evaluate the direction and rate of succession, and to modify the direction of change if development is away from the desired end point.

Project facilities will also affect the rates and patterns of succession of areas within their zone of influence. The differing sensitivities and responses of plant species to pollutants and changes in microclimate and drainage will result in the selective removal of sensitive species and a reduction of vigour of somewhat more tolerant species. This would change community composition, altering successional rates or patterns.

6.2 CURRENT LEVEL OF KNOWLEDGE AND DATA GAPS

6.2.1 Classification

No one method or approach to classification can be considered best without first considering the objectives and future uses of the information. Each system has strengths and weaknesses, advantages and disadvantages. Classifications are "human creations, serving different purposes, never sufficient in themselves, and usually to some extent complementary to one another" (Whittaker 1962).

A fundamental difference between Z-M and North American approaches is their sampling philosophy and methodology regarding size, number, and randomness of plots. Z-M relies on one "minimal area" plot per stand; North American studies usually involve several, randomly located, smaller plots, at least for understory species. In addition, North American and British investigators have developed plotless techniques and have concentrated on quantitative and statistical analysis (such as ordination and cluster analysis).

In recent years, these differences have become somewhat blurred. More North American studies are adopting the Z-M approach (particularly as adapted by V.J. Krajina and his students at the University of British Columbia, e.g., Hoefs et al. 1975). Stringer

(1976) used the sampling approach of Z-M in a vegetation survey of the AOSERP study area, but he classified the vegetation by the North American approach of dominants. In Europe, quantitative techniques are being used to help analyze and evaluate the results of Z-M classification (e.g., Maarel 1969; Shimwell 1972; Mueller-Dombois and Ellenberg 1974).

Although the units which result from different approaches are not directly comparable, both are useful and valid in helping interpret vegetation patterns. In his massive monograph on classification of natural communities, Whittaker (1962:155-156) concluded:

> "It may finally be observed that the cleavage between the ecological and phytosociological traditions is too deep-seated to be resolved by arbitrary standardization. Although it is easy to deplore lack of international agreement, ecological science may well have gained by the choice of one group to explore thoroughly the approach to communities through systematic classification, whereas others explored other approaches. Braun-Blanquet's formal classifications and ecologists' informal ones are not directly compatible with one another, but neither are they fully incompatible. Associations and dominance-types are different units; but some associations correspond to dominance-types, and some dominance-types and subtypes can be characterized by diagnostic species. Mutual understanding might increase if ecologists made more effective use of diagnostic species, and if phytosociologists made more explicit the place of formations and dominance-types in their system. It may further be expected that as more intensive analytical work, little concerned with classification as such, progresses in both traditions, the present differences will become less important. For now, the objective may be not so much full agreement as greater common understanding among ecological scientists of different interests and traditions."

Detailed AOSERP vegetation classification studies to date consist of those of Stringer (1976) and Thompson et al. (1978). Stringer (1976) conducted a rapid reconnaissance survey of the mature vegetation within part of the AOSERP study area. He

identified 10 major vegetation types using cluster analysis and named them on the basis of physiognomy and dominant overstory. Characteristic understory species were identified to the extent possible.

Thompson et al. (1978) subsequently developed 1:50 000 scale biophysical maps based on airphoto interpretation for about half the AOSERP study area. The vegetation legend was adapted from Stringer's types.

Stringer (1976) and Thompson et al. (1978) thoroughly discussed the limitations of their studies. Both involved insufficient field sampling with most data obtained at less than ideal times. Stringer's (1976) field survey was short and in late August. As a result, only a few samples could be collected on a limited area and many characteristic species may have been missed. Thompson et al. (1978) were unable to conduct ground surveys due to time limitations, and had to rely on Stringer's (1976) work, scattered data sources, and the interpreter's experience and expertise. In addition, the photos used were taken during flights in late October. This made the mapping more difficult and reduced the accuracy of identifying tree species and height and extent of crown cover. In addition to these problems, some of Stringer's (1976) clusters may be composites of different types, and there are an insufficient number of sites, particularly on recent burns and other disturbances.

6.2.2 Succession and Ecology

Succession--the development of the major physiogonomic types present on the AOSERP study area--appears to follow the general patterns, rates, and sequences of surrounding boreal forest areas. Specific details about understory species, sequences, roles, and rates of change, as well as site factors of soils and microclimate changes, however, are largely lacking.

The most detailed information exists for river and lake shores from studies of the Athabasca Delta (Dabbs 1971, Dirschl

1973) and along valleys of the Athabasca, Peace, and Slave rivers (Raup 1935). Numerous studies have been carried out in forested uplands and lowlands of surrounding areas, but the extent to which they are relevant to the AOSERP study area is unknown. These include studies in Wood Buffalo National Park (Raup 1935; Lacate et al. 1965), in the mixedwoods of Alberta (Moss 1932; Duffy 1964, 1965), in northwestern Alberta (Moss 1953b) and westcentral Alberta (Moss and Pegg 1963), in the boreal forest (LaRoi 1967b; Moss 1955), spruce forest (LaRoi 1967a), and spruce-fir forest (Achuff 1974), and at Candle Lake Saskatchewan (Swan and Dix 1966; Dix and Swan 1971).

Muskeg and related wetland types are the most complex. They have been extensively studied in many parts of the world, including areas near the AOSERP study area. Such nearby studies include those at Candle Lake, Saskatchewan (Jeglum 1968, 1971, 1973); swamp, moor, and bog forests in central Alberta (Lewis and Dowding 1926; Lewis et al. 1928); patterned fens in the Swan Hills of north-central Alberta (Vitt et al. 1975); and marshes and bogs in northwestern Alberta (Moss 1953a). Since wetlands are highly variable and their occurrence, existence, and development depends on such intricately interrelated factors as water level, chemistry, pH, water movement, and peat accumulation, it is not known whether information from these nearby sites is applicable. Stringer (1976), however, indicated that such areas should be evaluated on a site-by-site basis and Jeglum (1968) suggested using permanent quadrats over a period of time.

Several vegetation studies have been carried out in the AOSERP study area proper. Raup (1935, 1936, 1946, 1975) detailed the vegetation types and species along the Clearwater and Athabasca rivers. More recently, descriptive studies of vegetation types include Syncrude (1973), Lombard North (1974), and Stringer (1976).

Discussions of succession vary with the study. Those with great detail are usually specific to a site or area but this limits their usefulness to other geographical regions. Others are more general and apply to broad regions.

Knowledge of the understory is for the most part limited to distribution relative to the tree canopy under which it grows. Stringer (1976) emphasized the need for such knowledge. Rowe (1956) studied the role of understory species in the mixedwoods of Manitoba and Saskatchewan; however, regional differences in environment and species distribution (LaRoi 1967a) largely limits its application to similar parts of the AOSERP study area.

Ecological requirements of the principal tree species appear to be sufficiently well-known as a result of their economic importance and resultant silvicultural studies. Requirements of most understory species, however, appear to be insufficiently known. Productivity of forest stands is known to some extent but not specifically in the AOSERP study area.

In general, the effects of pollutants are not sufficiently well-known for most species on the AOSERP study area. Knowledge of the effects of pollutants released by developments in the AOSERP study area varies with the substance. This information is extensive but scattered throughout the literature (see, for example, Mudd and Kozlowski 1975). The levels and amount of exposure to SO_2 needed to cause visual damage to most tree species are generally known. The high sensitivity of numerous lichens and bryophytes to SO_2 has been extensively documented and they have been used as indicators of pollution. Studies have recently begun of the effects on vegetation dynamics as a result of the selective removal of species sensitive to SO_2 in central Alberta (Winner and Bewley 1978).

For general comparative purposes, rates and broad patterns of succession are sufficiently well-known from adjacent areas and require only limited additional studies to confirm their applicability to the AOSERP study area. For more specific application, intensive management, and effective classification and mapping, however, there is insufficient knowledge of vegetation dynamics, particularly with respect to understory species and overstory/understory relationships as site characteristics change during succession. Additional knowledge on successional and

autecological requirements is also needed where site reclamation objectives involve the establishment of specific desired end points.

6.3 RECOMMENDED STUDIES

6.3.1 Classification

Preliminary classification and mapping of vegetation on the AOSERP study area has used a biophysical approach. Initial large-scale mapping using physiognomic criteria supplemented by existing ground survey information (Stringer 1976) has been prepared by Thompson et al. (1978). This system cannot distinguish different herbaceous or low scrub vegetation types and identification of mixed tree populations is difficult. In addition, airphoto analysis alone cannot identify characteristics of the forest understory.

A biophysical approach appears to be most appropriate for meeting needs of AOSERP. It is flexible and open-ended. Properly planned and designed, it can provide and allow the organization of information useful for various land use and land management aspects including wildlife and reclamation. The existing information will need to be supplemented with extensive ground-truthing, particularly in areas not sampled by Stringer (1976). The studies should be multi-disciplinary, since detailed information on topography, hydrology, soil type, and surficial geology are required to properly evaluate the dynamic characteristics and interrelationships of the various plant communities. Such field sampling must be carried out at optimum times to ensure that all species are sampled.

A biophysical approach is capable of looking at the different scales and levels of detail required for the AOSERP study. Detailed site mapping can be carried out as required, to clarify and refine the regional scale data. Such detailed studies

will also be needed to test land management approaches, particularly those related to reclamation, in representative sites.

To date, vegetation classification studies have followed a traditional North American approach. It may prove beneficial to collect data on key sites so that floristic analysis techniques (Z-M) can be applied, if not now, in the future. This should not add excessively to any study carried out since data provided by most vegetation studies can be analyzed by Z-M methods, provided that all of the flora are identified (a requirement previously recommended by Stringer (1976) for the AOSERP study area) and the area sampled approaches Z-M minimal area criteria. A complete Z-M analysis of the AOSERP study area would be a massive, long-term effort and is not being recommended here. If the analysis were carried out on key sites, however, it would be possible to compare vegetation units and management techniques with those in other parts of the world.

6.3.2 Succession and Ecology

Data obtained for mapping and classification described above will provide much of the information needed for studies of succession and ecology, provided that burns of known ages are sampled. These data would identify pioneer and indicator species, and allow evaluation of how well regional succession knowledge applies to the AOSERP study area. They would also help clarify the dynamics of change, the ecological role of species and species groups, and the rates of change. More detailed site-specific studies, however, would be needed to arrive at desired reclamation end points. These would include knowledge of initial site conditions and how they must change to favour the desired end point.

Additional studies would be needed to evaluate the effects of differential species removal on succession and recovery. The role and importance of fungi and soil micro-organisms in nutrient cycling have not been evaluated in this study; they require additional study.

Key species likely to be affected by the project should be identified. These should include any desirable end-point species, candidate species for use in reclamation, and indicator species sensitive to the types of pollutants likely to be present in the project's zone of influence. For these key species, the literature should be reviewed in light of anticipated pollutant levels to determine their suitability and whether additional studies are needed.

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8. SELECTED ANNOTATED REFERENCES

Dirschl, H.J. 1973. Trends in vegetation succession on the Peace-Athabasca Delta. Section J in Ecological investigations. Peace-Athabasca Delta Project, Tech. App., Vol. 2, Edmonton, Alta.

With the completion of the W.A.C. Bennett Dam on the Peace River, a study was initiated to determine its effects on the vegetation of the Peace-Athabasca Delta, particularly through changes in water regime. This report examines effects on vegetational succession as it applies to deltas in general, and the Peace-Athabasca Delta in particular.

Delta dynamics and the formation of exposed sites including islands, point bars, oxbows, levees, perched basins, and emerging delta plains are briefly discussed. They form the basis for development of complex vegetation, the dynamics of which (at a given point in time) may be examined on sites of different ages. Natural events such as fire, drought, and flood modify vegetation dynamics as do artificial changes of water regimes.

On the Delta, major changes resulted from the greatly reduced spring floods since 1968. Sedge and grass meadows and shrub vegetation spread easily.

Five community types were recognized: aquatic, shore, meadow, shrub, and forest. These, combined with three major site types (the active delta, semi-active delta and inactive delta) lead to a branching network of successional pathways in which various species (or species groups) may dominate during the same seral stage at various locations. Two factors, seed supply at the time of germination and minute local differences in moisture and nutrient status, are identified as producing the diversity on what appear to be identical sites.

An outline of succession as it is believed to operate on the various Delta sites is presented as are the projected successional rates. Two conclusions are drawn: (1) that succession on the Delta is primarily controlled by water regime; and (2) that vegetation changes under falling water levels proceed very rapidly in the initial stages but progressively more slowly through the shrub and forest types.

Dix, R.L., and J.M.A. Swan. 1971. The roles of disturbance and succession in upland forest at Candle Lake, Saskatchewan. Can. J. Bot. 49:657-676.

Eighty-nine upland forest stands were selected to cover the ranges of tree species composition, stand ages, understory composition, and site in the area. The role of each tree species as a pioneer, transient, or self-maintaining component of the forest was determined from the number of stems, their vigor, and distribution in tree, sapling, and seedling strata among all stands and from growth increment cores of trees and saplings in 39 stands. Conclusions are drawn regarding the species likely to dominate different sites following severe fire and the kinds of vegetational change likely to occur on them between disturbances. Changing patterns in the non-arboreal vascular flora, moss, and lichen cover were related to changes in tree species composition with site and time. The forest and its environment are linked in an irregular "pulse" strategy of alternating disturbance and regrowth that repeatedly rejuvenates the growing stock. (Authors' abstract)

Heinselman, M.L. 1973. Fire in the virgin forests of the boundary waters canoe area, Minnesota. Quatern. Res. 3:329-382.

Fire largely determined the composition and structure of the presettlement vegetation of the Boundary Waters Canoe Area as well as the vegetation mosaic on the landscape and the habitat patterns for wildlife. It also influenced nutrient cycles, and energy pathways, and helped maintain the diversity, productivity, and long-term stability of the ecosystem. Thus the whole ecosystem was fire-dependent.

At least some overstory elements in virtually all forest stands still date from regeneration that followed one or more fires since 1595 A.D. The average interval between significant fire years was about 4 yr in presettlement times, but shortened to 2 yr from 1868 to 1910 during settlement. However, 83% of the area burned before the beginning of suppression programs resulted from just nine fire periods: 1894, 1875, 1863-4, 1824, 1801, 1755-9, 1727, 1692, 1681. The average interval between these major fire years was 26 yr. Most present virgin forests date from regeneration that followed fires in these years. Significant areas were also regenerated by fires in

1903, 1910, 1936, and 1971. Most major fire years occurred during prolonged summer droughts of sub-continental extent, such as those of 1864, 1910, and 1936. Many fires were man-caused, but lightning ignitions were also common. Lightning alone is probably a sufficient source of ignitions to guarantee that older stands burned before attaining climax. Dry matter accumulations, spruce budworm outbreaks, blowdowns, and other interactions related to time since fire increase the probability that old stands will burn. Vegetation patterns on the landscape were influenced by such natural firebreaks as lakes, streams, wetlands, and moist slopes. Red and white pine are most common on islands, and to the east, northeast, or southeast of such firebreaks. Jack pine, aspen-birch, and sprout hardwood forests are most common on large uplands distant from or west of such firebreaks.

A Natural Fire Rotation of about 100 yr prevailed in presettlement times, but many red and white pine stands remained largely intact for 150 to 350 yr, and some jack pine and aspen-birch forests probably burned at intervals of 50 yr or less. There is paleoecological evidence that fire was an ecosystem factor before European man arrived, and even before early man migrated to North America. Probably few areas ever attained the postulated fir-spruce-cedar-birch climax in postglacial times. To understand the dynamics of fire-dependent ecosystems fire must be studied as an integral part of the system. The search for stable communities that might develop without fire is futile and avoids the real challenge of understanding nature on her own terms.

To restore the natural ecosystem of the Canoe Area fire should soon be reintroduced through a program of prescribed fires and monitored lightning fires. Failing this, major unnatural, perhaps unpredictable, changes in the ecosystem will occur. (Author's abstract)

Jeglum, J.K. 1968. Lowland vegetation at Candle Lake, southern boreal forest, Saskatchewan. Ph.D. Thesis. Dept. Plant Ecology, Univ. Saskatchewan, Saskatoon.

The purpose of the study was to determine principal vegetational and environmental interrelationships of lowlands of an area 32 x 65 km centering around

Candle Lake, Saskatchewan, located in the southern region, or Mixedwood Section, of the boreal forest.

Quantitative measurements of trees, tree saplings, tree seedlings, shrubs, herbs and dwarf shrubs, and mosses and lichens were obtained in 119 stand-samples. Measured and observed environmental characteristics included water level, conductivity and pH for water samples, depth of peat and principal horizons, pH and von Post decomposition ratings for the upper 15 cm of moist peat, and observations on physiographic location.

An informal, hierarchical classification was developed to obtain readily recognizable types for description and comparison. Nine physiognomic groups were established on the basis of overall appearance: Emergent Fen (Reedswamp), Broad-leaved Sedge Fen, Narrow-leaved Sedge Fen, Tall Shrub Fen, Low Shrub Fen, Wooded (Tamarack) Fen, Intermediate Fen-Bog, Treed Bog (Muskeg), and Moist Forest. These groups were further segregated into 36 dominant types, and described in terms of vegetation and environment.

A two-dimensional summary diagram was developed by plotting the units according to their mean or slightly revised mean water levels and conductivities. In addition to illustrating moisture and nutrient relationships, the model was shown to account for a large proportion of the vegetational variation among the units. The evidence for this was a highly significant correlation between similarity indices ($2w / a + b$) and inter-unit distances on the diagram for a number of randomly chosen pairs of dominance types; concentrically diminishing quantitative values from a model high for numerous species plotted in the diagram; and meaningful patterns for several other phytosociological attributes plotted in the diagram. This suggested that moisture and nutrient regime were the two major factors influencing lowland vegetation at Candle Lake.

Two subsidiary factors acting to modify moisture and nutrients were the interrelated aspects of peat accumulation and drainage blockage. For fen vegetation there was a highly significant, negative correlation between peat depth and conductivity. Although not demonstrated, there was undoubtedly a similar relationship between depth of *Sphagnum* and nutrient status. Four drainage systems which represent increasing drainage impedance were recognized: drained fens with distinct channels, drained fans without distinct channels, undrained fens, and bogs.

Finally, vegetational patterns in the landscape were described in relation to the drainage systems. These included zonations, complexes of beach ridges and swales, ripplemarks in fen drainageways, and forest islands. Bogs were usually positioned as topographically-oriented, sloping terraces between upland and fen, although some small, flat raised bogs were found. The scarcity of raised bogs was explained by the dry, subhumid climate prevailing at Candle Lake. (Author's abstract)

Jeglum, J.K. 1972. Boreal forest wetlands near Candle Lake, central Saskatchewan. I. Vegetation. The Musk-ox 11:41-58.

Quantitative and qualitative data were obtained for vegetation and environment in 119 wetland, predominantly peatland, stands. An informal, hierarchical classification consisting of five main categories (cf. vegetation formations), nine physiognomic groups, and 36 dominance types is presented. Description emphasizes the physiognomic groups, and these are compared and contrasted among themselves, and with similar types described in the literature for the same and adjoining regions. (Author's abstract)

Jeglum, J.K. 1973. Boreal forest wetlands near Candle Lake, central Saskatchewan. Part II. Relationships of vegetational variation to major environmental gradients. The Musk-ox 12:32-48.

The purpose of the study is to relate vegetational variation in Candle Lake wetlands to major environmental gradients. Environmental ordinations are developed by plotting types and stands in terms of selected single measures of the environment. Principal component ordinations are used to derive component axes of vegetational variation, which are subsequently correlated with the single measures. Finally, major vegetational patterns in the landscape are described. The emphasis throughout the analysis is on the proportional influence of the main complex-gradients--moisture, nutrient and disturbance regimes--on principal lines of vegetational variation and on observed vegetational patterns in the landscape. (Author's abstract)

Kelsall, J.P., E.S. Telfer, and T.D. Wright. 1977. The effects of fire on the ecology of the boreal forest, with particular reference to the Canadian north: a review and selected bibliography. Can. Wildl. Serv. Occas. Pap. No. 32.

This review analyzes literature relevant to effects of fire on the Boreal Forest, and on its related wildlife resources, with particular reference to the Canadian North. The selected bibliography contains the more recent and historically important references and is not all-inclusive. Because of a paucity of material pertinent to the forests of the Northwest and the Yukon territories, it has been necessary to extrapolate information from other areas. Alaskan publications have been particularly useful.

It was concluded that fire is the most important factor influencing the ecology of the northern Boreal Forest; that fire and the resulting forest mosaic are natural features of long standing; and that the Boreal Forest can be characterized as a fire-dependent ecosystem. Trees, other plants, birds, mammals, and other animals of the forest have evolved in response and adaptation to the frequency, extent, and intensity of fire. With some possible exceptions, a mosaic of varied successional stages in the Boreal Forest provides a richer habitat for a more varied and abundant fauna than does the monotypic spruce forest characteristic of unburned areas. Specific attention is given to fish, birds, and mammals--particularly to important species of game and furbearers--and to such characteristics of the northern forests as the presence of permafrost, the soils, and the characteristics of unique vegetation. The basic characteristics of different types of fires are also described. (Authors' abstract)

Lewis, F.J., and E.S. Dowding. 1926. The vegetation and retrogressive changes of peat areas (muskegs) in central Alberta. J. Ecol. 14:317-341.

A description of the vegetation, physical features and retrogression of three muskeg areas within 30 miles of Edmonton, Alberta is given.

Vegetation is described on the basis of dominant and subordinate species with some discussion of abundance, spatial distribution, and relations to topography.

Cores were taken to determine the nature and depth of peat and underlying materials. Water samples were analysed for pH, minerals, and plant matter.

Results of the coring indicated that the areas had initially been dominated by typical aquatic plants: *Hippuris* spp., *Potamogeton* spp., *Cyperus* spp. and *Scirpus* spp. Only a few centimetres of *Scirpus* peat were present under 3 to 4 m of *Sphagnum* in some places, indicating an early and relatively long term invasion.

At the Stony Plains location, a pH of 4.5 in water squeezed from *Sphagnum* versus pH 9 in open water, coupled with dead and dying *Sphagnum*, water analyses and other vegetation changes indicated that mineral spring water in one end of the area is causing retrogression. Vegetation changes, as reflected by peat cores and the tendency for *Sphagnum* replacement, also indicated that retrogress on in peat basins can be caused by fire and climatic changes.

Lewis, F.J., E.S. Dowding, and E.H. Moss. 1928. The vegetation of Alberta. II. The swamp, moor, and bog forest vegetation of central Alberta. J. Ecol. 16:19-70.

The types of swamp, moor and bog forest vegetation in three of the phytogeographical regions of central Alberta have been described. The areas lie in morainic basins of varying size, and the blue glacial clay under the peat deposits contains numerous mosses and the seeds of water plants inhabiting the lakes before the formation of the low-moors and high-moors which now occupy these basins.

The pH of the low-moors varies from 5.0 to 6.5 and the high-moors 4.0 to 5.5. Analyses of the clays and the free water in types of swamps, low-moors and high-moors are given.

The vegetation is described from a regional point of view under the three climatic climax formations characteristic of central and northern Alberta, viz., the Cordilleran Forest, Northern Forest, and Poplar Parkland. In the Cordilleran Forest area the three most widely distributed formations banding lake margins are low-moors (Cariceta), birch bogs and bog forest. Centrifugal growth of *Sphagnum-Andromeda* (the earliest association of the *Sphagnum* succession) is rare, and has been met with in only one basin. Birch bogs are

developed as primary associations in large deep basins where much of the ground is covered with *Hypnum revolvens* with a flora in which *Ericaceae* are absent. Larch is associated with the birch, the latter usually being confined to the ridges formed by the long horizontal roots of the larch. The floras of the ridges and the flat depressions between are strongly contrasted. Mature bog forest formed of old black spruce with a floor of *Hypnum crista-castrensis* L. and *Hylocomium splendens* and a scanty non-ericaceous flora forms the climax of the bog succession. The general succession in the Northern Forest resembles in broad features that of the Cordilleran Forest. Marginal muskegs encroaching on central low-moor (Cariceta) are frequent and are present as primary successions in some basins, *Sphagnum* spreading centripetally into the Caricetum. Marginal muskegs are also present as a secondary succession, and in such cases mounds of the original high-moor are often found scattered over the secondary low-moor; their survival being due to irregular burning. Small muskegs in which the original *Sphagnum*-ericaceous vegetation has entirely disappeared occur near the southern boundary of the Northern Forest. White spruce and poplar have occupied these areas.

In the Parkland reed-swamp and low-moors are usually associated with sloughs and lakes. Swamps are formed of various associations of rushes, sedges and grasses, while low-moors may be dominated by Cariceta, Saliceta or Gramineta. The high-moors are generally at the *Ledum* moor stage and examples of climax bog forest are rare. The succession of associations within the various formations are described, and the effects of burning, drainage, mowing, grazing and other factors are discussed.

The destruction of high-moors by the influx of springs rich in calcium salts is described, and the activity of algae acting under such conditions has resulted in extensive mineral deposits ranging as high as 80 per cent calcium carbonate. (Authors' summary)

Moss, E.H. 1953a. Marsh and bog vegetation in northwestern Alberta. Can. J. Bot. 31:448-470.

Swamp, marsh, wet meadow, saline meadow, *Drepanocladus* bog, and *Sphagnum* bog are characterized and related aquatic vegetation is described briefly. There is succession from different kinds of swamp and marsh, through wet meadow, to *Agropyron-Carex* grassland and

to various wooded communities, and also of marsh, through *Drepanocladus-Carex* bog to a *Larix laricino* association. The main bog sere of the region is initiated by some kind of aquatic or marsh phase and passes through *Sphagnum* bog stages to bog forest (*Picea mariana*) climax. Ecological aspects of *Sphagnum* species are considered in relation to succession and a regeneration cycle. Retrogression caused by burning is described for marshes, bogs, and bog forests. Many bogs in the northern part of the region have large mounds and ridges that retain frozen peat below the surface mantle during the summer. The significance of these permafrost areas is discussed. Brief consideration is given to phytogeographical features of the region. (Author's abstract)

Moss, E.H. 1953b. Forest communities in northwestern Alberta. Can. J. Bot. 31:212-252.

Spruce, tamarack (larch), balsam fir, pine, and poplar communities of the region are described in terms of floristic composition and ecological relationships. The white spruce (*Picea glauca*) association is regarded as the climax type of the region. Of four phases or faciations presented by the white spruce association, the feather moss faciation appears to be the climax to which the other faciations tend to develop. Two black spruce (*Picea mariana*) communities are recognized, the black spruce-feather moss association and the black spruce-peat moss association. Of these, the former is characterized by "feather mosses" such as *Hylocomium splendens* and has developed on relatively level terrain without much peat formation, whereas the latter has a *Sphagnum* floor and has arisen in definite depressions through acid bog stages with the production of considerable peat. The black spruce-bog moss community is interpreted as subclimax, with natural succession to the black spruce-feather moss association. The tamarack (*Larix laricina*) community has many features in common with the black spruce-peat moss association but differs markedly, not only in its dominant species, but because of its development from a *Drepanocladus-Carex-Betula* bog under persisting wet conditions. Succession to black spruce commonly occurs. Balsam fir (*Abies balsamea*) is relatively rare in the region and usually grows in mixed stands with white spruce, paper birch, aspen, and balsam poplar. Two divisions of the pine association are recognized, the jack pine (*Pinus banksiana*) and the lodgepole pine (*P. contorta* var. *latifolia* consociations. For each of these, two phases are

described, the pine-feather moss faciation on the more shaded sites and the pine-heath faciation on the more open and drier areas. Knowledge of the ranges of these two pines in northern Alberta and concerning hybrids between the species is extended. The poplar association, classified as aspen (*Populus tremuloides*) and balsam poplar (P. *balsamifera*) consociations, is considered in relation to other vegetation, especially prairie grassland and white spruce. Encroachment of aspen poplar upon native grassland is counteracted by various factors, notably burning. Natural succession of poplar and pine to white spruce is impeded chiefly by forest fires. Some attention is given to phytogeographical problems of this transition region. (Author's abstract)

Moss, E.H. 1955. The vegetation of Alberta. Bot. Rev. 21:493-567.

This paper discusses previous floristic work in the region and gives a general description of the climate, physical features, geology and soils.

Alberta presents a complex phytogeographical setting due to the meeting of cordilleran, boreal, steppe, and forest elements within the province, coupled with Pleistocene glacial effects on the flora. A brief discussion of these is presented to provide a background for understanding the vegetation types.

Major vegetation types discussed are Prairie, Parkland, Deciduous forest, Boreal forest, Cordilleran forest, Alpine, Marsh and Reed Swamp, and Miscellaneous types. Associations within each type are discussed as are the associated species, location, and site characteristics and the dynamics of change as reflected in the literature. The presentation is generally in terms of communities, succession, and monoclimax; however, for certain mountain forests, the continuum concept and the climax as a variable pattern seemed more appropriate.

Attention is drawn to management and conservation problems relating to prairies and forests and the current attitudes of those investigating and administering the areas.

Moss, E.H., and G. Pegg. 1963. Noteworthy plant species and communities in west-central Alberta. Can. J. Bot. 41:1079-1105.

This paper reports significant extensions of range for 71 vascular species and discusses the occurrence of several of these plants in relation to postglacial development of the flora of westcentral Alberta. Some attention is paid to the coniferous vegetation of the region, especially those faciations in which certain of the more interesting species occur. The alpine fir and black spruce faciations are regarded as edaphic climax types in the upland forest. Species new to Alberta include the "eastern" *Rhynchospora capillacea*, the rare *Sparganium glomeratum*, and the "Pacific" *Streptopus streptopoides* var. *brevipes*. Two other "Pacific" species, *Angelica genuflexa* and *Tiarella trifoliata*, previously known in the area from isolated collections, are now reported as widespread and locally abundant. Floristic data support the hypothesis of a fluctuating ice-free corridor as a refugium in western Alberta during the late Wisconsin or soon thereafter, and point to Manitoba-Saskatchewan-Alberta as a vast meeting ground of "eastern" and "western" biota. (Authors' abstract)

Raup, H.M. 1935. Botanical investigations in Wood Buffalo Park. Can. Dept. Mines, Natl. Mus. Can. Bull. No. 74.

This paper briefly reviews and summarizes the history of plant collections in the Wood Buffalo National Park area of northcentral Alberta. Topography, soils, climate and geological history of the area are generally described.

Representative locations for five major types are discussed. The primary and secondary species and the observed variations of site and vegetation within each are elaborated.

The Upland Forest type consists of stands dominated by *Picea glauca* and *Pinus banksiana* with varying amounts and mixtures of deciduous tree species, depending on the fire history. Detailed diagrams of vegetation zonation are given for the Upland Lake Shire Vegetation types and the aquatic and shrub associations are discussed. The Muskeg type includes aquatic, shoreline, bog, shrub, and tree associations. The Semi-open Prairie vegetation exists as two main types based on soil-water holding capacity. Heavy soils were dominated by *Calamagrostis canadensis*, *Poa pratensis* and *Carex atherodes* and light

soils by *Agropyron trachycaulum, Stipa comata, Koeleria cristata, Carex foenea* and/or *C. obtusata*. The Peace-Athabasca Delta region is discussed in terms of delta plains, local river deposits and slough and wet meadow vegetation. Hydrarch succession diagrams from aquatic to forest vegetation are given for river deposits and plains, creeks and sloughs.

The flora of the Granite Hills is discussed separately because it is distinct from the rest of the area.

Raup, H.M. 1946. Phytogeographic Studies in the Athabaska-Great Slave Lake region. II. J. Arnold Arboretum 27:1-85.

The forests of the Athabaska-Great Slave Lake region are described in seven types (pp. 37-61). The first three are composed principally of white spruce, *Picea glauca* s. l., but differ in composition, structure, history, and geographic position. The remaining four are of jack pine, balsam fir and white spruce, black spruce and lodgepole pine, and bog forest of black spruce. Park-like white spruce forests have their greatest development near the arctic timber line, on some of the most youthful land surfaces which the region affords--surfaces exposed at the retreat of the last glacial ice from the lake region and at the drainage of the last glacial lakes. Flood plain white spruce timber is concentrated principally on the great flood plains and deltas of the Athabaska, Peace, and Slave Rivers, also on very young surfaces. Upland mesophytic forests of white spruce are mainly on deposits of glacial till and outwash that overlie rocks of Paleozoic or Cretaceous age. Nearly all of them are on surfaces exposed at earlier stages of ice and lake withdrawal (pp. 24-30). These surfaces are, in general, progressively older from northeast to southwest. Jack pine forests are most extensively developed over the pre-Cambrian rocks of the Laurentian Plateau. They are bounded on the northeast by the park-like white spruce type and on the southwest by flood plain and upland mesophytic white spruce forests. In this region the pine is regarded as a primary type, but in the upland mesophytic spruce it also occurs extensively as a fire tree, along with trembling aspen and balsam poplar. Forests of balsam fir and white spruce are confined to the flood plain of the Athabaska and Clearwater Rivers, in the southern part of the region. Black spruce-lodgepole pine

timber has been found thus far only on the Caribou Mt. Plateau north of the lower Peace River. Bog forests of black spruce and larch are widespread in the region, with no obvious relation to age of surface, but with some concentration on the Laurentian Plateau where undrained, bog-filled depressions are extremely numerous (pp. 61-64).

Floristically the region is a part of the meeting-ground of northern Rocky Mountain and eastern Canadian forest elements (pp. 72-74). It is presumed that the late Wisconsin (W_3), ice advance destroyed the interglacial connections between these eastern and western elements, and that the relics thus isolated are still in process of being rejoined. The least mesophytic species in the region-the spruces, white birches, larches, and aspens-probably were least restricted by peri-glacial conditions and have been the most successful at merging their relic populations. The most mesophytic species, the balsam first, have been least successful, and apparently have not yet overlapped the ranges of their eastern and western components. The pines and probably the balsam poplars appear to be intermediate between the above categories (pp. 74-75). Eastern and western elements are still taxonomically distinct among the firs and pines, but among the species complexes in which merging has occurred only varietal distinctions are possible, with an abundance of intermediate forms.

The advance of forests into the Athabaska-Great Slave Lake region is thought to have been conditioned by the progressive amelioration of climates, by the progressive availability of land surfaces and suitable soils, and by the availability of tree populations from which the immigrants could come (pp. 72-73). The order of appearance of these immigrants was in turn conditioned by their general position in the Canadian forests with regard to subarctic climatic zones (pp. 64-72), and by the extent to which their migratory capacities were altered by the vicissitudes of the late Wisconsin glacial period (p.74).

The earliest forests are thought to have been of white spruce from the foothills of the northern Rocky Mountain region, and to have entered the lake country from the southwest and west. The eastern elements are presumed to have come later, the jack pines occupying the sterile soils of the Laurentian Plateau, and the eastern white spruces interbreeding with the western forms (var. *albertiana*) on the Alberta Plateau and the river lowlands. The park-like white spruce type is

thought to be a relic of the early western population, more or less isolated by the jack pine belt which has been preserved and accentuated by the sterility of the Laurentian area (p. 75).

Evidence is presented which indicates that there were no forests of large extent in central or southern Alberta or in Saskatchewan during late Wisconsin time, and that they did not appear in the southern part of the Mackenzie basin until after the final disappearance of the ice from Great Slave Lake and the drainage of the 800-foot post-glacial lake (pp. 75-78). It is thought that these events may have occurred as late as 7000-9000 years ago, bringing the advent of forests to the Athabasca-Great Slave Lake region into the period of the widely postulated post-glacial climatic optimum (pp. 69-71). (Author's abstract)

Rowe, J.S. 1956. Uses of undergrowth plant species in forestry. Ecology 37:461-473.

No system of describing stands in general terms has hitherto been available for the southern boreal forest of Manitoba and Saskatchewan. A simple scheme based on the physiognomy of the undergrowth and on moistness of site is outlined.

As an aid to stand description, a vegetation table is presented, showing the positions of about 200 common forest species relative to one another so far as their heights and their moisture preferences are concerned. For field use, a sheet has been drawn up in the form of this table, and the species occurring in plots or stands under study are checked off on it. The resulting scatter pattern provides a basis for the interpretation of site moistness, successional status of the community, density of canopy, and so forth.

Some of the commoner forest communities in the southern boreal forest of Manitoba-Saskatchewan are briefly described using the moisture-physiognomy scheme, and mention is made of some of the prominent species.

The possibility of using the groupings of species in the five moisture series, as shown in the vegetation table, for the interpretation of moisture of site is examined, and a method of working out a Vegetation Moisture Index is proposed. This Index is compared with moisture estimates derived from the study of soils and topography, and a good correspondence is shown.

It is finally suggested that the method used in working out an index of moistness from the plant species present on a particular site could also be used to derive indices of soil fertility and ecoclimate for use in stand description and in forestry research. (Author's summary)

Rowe, J.S. 1961. Critique of some vegetational concepts as applied to forests of northwestern Alberta. Can. J. Bot. 39:1007-1017.

The application, by R. Plochmann, of certain European silvicultural and ecological concepts in the study and description of forests of northwestern Alberta is examined. His ideas of unidirectional succession to the single climax forest are criticized on the grounds that concepts such as succession and climax must always be related to specific terrain. Every forest community, and indeed every vegetational community, is the botanical part of a unique geographic ecosystem which gives it meaning, and it is neglect of the geographic framework which has led to the false assumptions that forest communities can be studied as things-in-themselves, and that vegetational concepts derived in one region can be transplanted unchanged to others. (Author's abstract)

Rowe, J.S. and G.W. Scotter. 1973. Fire in the boreal forest. Quatern. Res. 3:444-464.

The boreal forest in North America owes much of its floristic and faunistic diversity to periodic fires ignited by lightning and by man since he appeared on the scene. The indirect evidences of burning in vegetation and soils, and recent direct observations of fires, are reviewed. Fire is shown to exert a significant effect on vegetational composition, on soil chemical properties and thermal regime, and on animal populations through the particular mosaic of habitats created. In turn, fire is itself influenced by the nature of geographic landscape ecosystems according to their surface forms, accumulations of organic materials, and susceptibility to drought. It is concluded that fire should be viewed as a normal ecological process in the boreal forest. A thorough understanding of its long-term role in terrestrial and aquatic ecosystems is needed. (Authors' abstract)

Stringer, P.W. 1976. A preliminary vegetation survey of the Alberta Oil Sands Environmental Research Program study area. Prep. the Alberta Oil Sands Research Program by Interverda Plant Systems Ltd. AOSERP Report 4. 108 p.

Between 18 August and 3 September 1975, 84 homogeneous stands chosen as representative of the major vegetation types were sampled in the Alberta Oil Sands Environmental Research Program (AOSERP) study area (56°21' - 58°00' N and 110°50' - 112°00' W). The structure and species composition of each was described by assigning to each understory species a cover-abundance value, measuring strata heights, and by obtaining, where appropriate, quantitative data on the tree stratum.

The 84 stands were classified on the basis of overall species similarity by means of cluster analysis. The clusters resulting from the analysis were readily identifiable as distinct vegetation types and were therefore distinguished on the basis of general species composition rather than by the more usual weighting of the tree stratum.

Ten vegetation types were identified: Fen; Sandbar Willow Scrub; Tall River Alder-Willow Scrub; Tall Willow Scrub; Bottomland Balsam Poplar Forest; Upland White Spruce-Aspen Forest; Black Spruce Bog Forest; Semi-open Black Spruce-Tamarack Bog Forest and Muskeg; Lightly Forested Tamarack and Open Muskeg; Jack Pine Forest.

There were also a number of ill-defined clusters and several consisting of a few stands only. This suggests that probably more, as yet inadequatly sampled, vegetation types exist. The findings of this study correlate well with the vegetation units indicated on the most recent forest cover maps.

Bryophytes and lichens were important components of many of the vegetation types. They often formed the bulk of the terrestrial plant biomass and were sometimes quantitatively more important than the vascular species, especially in mesic, closed-canopy coniferous forest, xeric jack pine forests, fens and muskegs. Many of the terrestrial species are sensitive indicators of the total environment and as such can be important in community classification.

Many lichens and bryophytes, especially corticolous species, are also sensitive indicators of air pollutants such as sulphur dioxide.

In future studies on mapping the AOSERP study area the following points should be noted. First, if anything more than a broad, physiognomically based mapping is to be attained, photointerpretation must be accompanied by extensive ground truth surveys.

Existing black and white imagery is of limited use for wetland and herbaceous vegetation. It is most useful for obtaining a rapid mapping of the major topographic features and of physiognomically defined vegetation types. Color and color infrared (false color) photographs used in conjunction are much more useful, enabling additional vegetation types, especially herbaceous ones, to be distinguished. A combination of true and infrared color aerial photography supplemented by the limited ground surveying possible may be the only feasible way of obtaining sufficient data on the extensive areas of wetland vegetation.

Ideally mapping of the vegetation should be done only after the dynamics of the communities and their relationship to the physical environment have been determined as far as possible, particularly in wetlands.

Finally, since most plants in the area are in flower between late July and late August, it is essential that future studies make maximum use of this very limited season. (Author's abstract)

Viereck, L.A. 1973. Wildfire in the taiga of Alaska. Quatern. Res. 3:465-495.

The taiga of Alaska consists of a vegetation mosaic resulting primarily from past wildfires. Today, both lightning- and man-caused wildfires burn an average of 400 000 hectares annually, creating vast areas of successional ecosystems. However, although the number of reported fires is increasing, fire control is becoming more effective in limiting the average size of fires and the total area burned. One of the important influences of fire in the taiga ecosystem is its effect on permafrost and the soil nutrient cycle. Construction of firelines in permafrost areas has a greater effect on soil erosion and siltation than does the fire itself. Some wildlife species, such as moose and snowshoe hare, depend upon fire and its resultant successional plant communities, whereas fire may have deleterious effects on caribou winter range. Fire has both positive and negative effects on aesthetic and recreational values. Fire has always been a part

of the Alaskan taiga ecosystem; if it is totally excluded from the environment, some major ecological changes will result. Fire-suppression alternatives are discussed and additional research on fire effects suggested. (Author's abstract)

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4.	VE 2.2	A Preliminary Vegetation Survey of the Alberta Oil Sands Environmental Research Program Study Area
5.	HY 3.1	The Evaluation of Wastewaters from an Oil Sand Extraction Plant
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